Volume LXXI Number 3

THE BOTANICAL GAZETTE

Editor: JOHN M. COULTER

MARCH 1921

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THE BOTANICAL GAZETTE

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EDITED BY

JOHN M. COULTER

With the assistance of other members of the botanical staff of the University of Chicago

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VOLUME LXXI NUMBER 3

THE
BOTANICAL GAZETTE

MARCH 1921

LEAF SPOTS OF THE ELM

L. E. MILES

(WITH PLATES VIII–X AND ONE FIGURE)

Introduction

About eighteen species of the genus *Ulmus* are known (2), widely distributed throughout the cold and temperate regions of the Northern Hemisphere. Six of these species, *U. americana*, *U. fulva*, *U. racemosa*, *U. alata*, *U. serotina*, and *U. crassifolia*, are native to America and occur naturally from Labrador to southern Mexico. None, however, occur west of the Rocky Mountains. *U. alata*, *U. crassifolia*, and *U. serotina* are tender and do not grow well in the northern states, but are quite extensively used for lawn and avenue trees in the south. *U. americana*, the most widely distributed American species, occurs in practically every state east of the Rocky Mountains, and in Canada. It is the most characteristic tree of the northeastern states, and is very widely used for street planting and as an ornamental tree for lawns.

Among the fungous enemies of the elm are a number of forms which cause leaf spots, the most important of which will be discussed in this paper. Ordinarily none of these diseases is of much importance economically, but in severe cases they may injure the tree materially by causing premature defoliation. This saps the vigor of the tree, and if the severe attack is repeated during a number of consecutive seasons, may even result in its death, or at

least may weaken it to such an extent that it is not able to withstand the adverse factors in its environment. In a nursery of young elm trees these leaf spots may do much more damage than when they occur on older trees.

Most important American leaf spot

Distribution and history

Chief among the fungi causing leaf spots of the elm in this country is *Gnomonia ulmea* (Schw.) Thüm. This disease, known as the elm leaf spot or elm leaf scab, occurs most commonly on

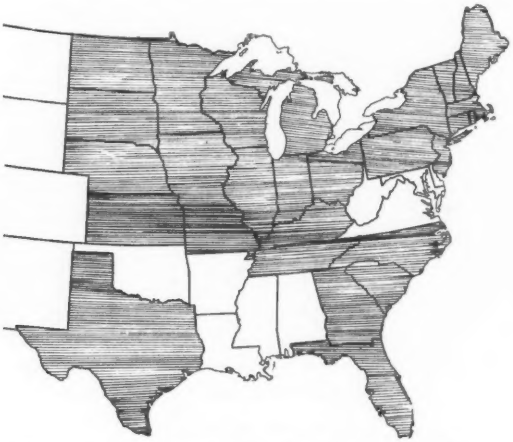

Fig. 1.—Distribution of *Gnomonia ulmea* in United States

U. americana, and is found in greater or less degree throughout the entire range of its host. The writer has examined exsiccati specimens of it which were collected in New York, Massachusetts, Vermont, Maine, New Hampshire, Rhode Island, Connecticut, Pennsylvania, Ohio, Michigan, Indiana, Illinois, Wisconsin, North Dakota, Iowa, Nebraska, South Dakota, Missouri, Kentucky, Tennessee, North Carolina, Georgia, South Carolina, and Texas, as well as several from Canada. Text fig. 1 gives a better idea of its wide distribution than does this list of states. It is more than probable that it occurs also in the remainder of the states east of

the Rocky Mountains, but has not been reported. In addition to the normal host, *U. americana*, specimens have been examined on *U. fulva*, *U. alata*, *U. crassifolia*, and *U. racemosa*, and it is quite probable that it may occur also on *U. serotina*, the only other American species. It has not been seen on any European or other foreign elm, however, collected either in this country or abroad, nor is there any account in literature of its occurrence on such. It may be concluded, therefore, that this fungus is strictly an American species.

The fungus was first described by SCHWEINITZ (**34**) as *Xyloma ulmeum*, in 1818, on leaves collected at Aiken, South Carolina. His material was immature, and consequently his description was incomplete and inadequate. Fig. 7 is a leaf from the type collection from which his description was taken. This specimen is one of SCHWEINITZ' exsiccati in the Museum of the Academy of Natural Sciences at Philadelphia. Comparison of this figure with figs. 3–5, showing infected leaves collected by the writer, indicates that the fungus with which SCHWEINITZ worked and the one discussed in the early part of this paper are identical.

A few years after SCHWEINITZ' original description, FRIES (**19**) described a disease of the American elm as caused by *Sphaeria ulmea* Fr., but gave *Xyloma ulmeum* Schw. as a synonym, showing that he had seen SCHWEINITZ' previous description and recognized that he was dealing with the same organism. His description added but little to the earlier one of SCHWEINITZ. The next change in the taxonomic position of the fungus was made in 1878 by VON THÜMEN (**39**) when he placed it in the genus *Gnomonia* without explanatory comment or additional description. In his *Sylloge Fungorum* SACCARDO seems to have accepted this change with some reservations, since he placed the fungus in the section Dubiae of the Sphaeriales, under the name *Gnomonia ulmea* (Schw.) Thüm., without, however, explaining his reasons for doing so.

In 1892 ELLIS and EVERHART (**16**) made a further change in the name and taxonomic position of the fungus, apparently without being acquainted with the previous work of VON THÜMEN, since they made no mention either of his name or of *Gnomonia* in

their account of the synonymy of the organism. They called it *Dothidella ulmea* (Schw.) E. and E., thereby placing it among the Dothidiales, although they acknowledge that it is "anomalous on account of its ascigerous cells assuming the characters of perithecia." In 1915 THIESSEN and SYDOW (**38**), in a monograph of the Dothidiales, excluded it from that group and referred it back again to *Gnomonia* in the Sphaeriales, where it had previously been placed by VON THÜMEN. In addition to these various names, the fungus has been much confused by American plant pathologists and mycologists with an organism causing a leaf spot of European elms in Europe, *Systremma Ulmi* (Schleich.) Thiess. and Syd. (**38**), to which it has a superficial resemblance, and it has often been collected and reported under one or another of various lists of synonyms pertaining to that fungus.

In 1901 and 1902 STONE and SMITH (**37**) from Massachusetts reported attempts at controlling the disease by spraying with Bordeaux mixture, referring to the fungus as *Dothidea Ulmi* (Duv.) Wint., a synonym of *Systremma Ulmi*, in the first paper, and as *Dothidella ulmea*, a synonym of *Gnomonia ulmea*, in the second, although they made no reference to the discrepancy. In 1910 GÜSSOW (**21**) reported it from Canada as extending back upon the petioles of young shoots to their tips, which twisted downward and finally died. He stated that in no case did the young shoots so infected recover. In this same year CLINTON (**8**) from Connecticut reported that by July or earlier some trees had shed almost all their leaves. He stated that these trees later put forth a new crop of foliage which was entirely free from the disease, but that the other trees, not so severely infected in the beginning, showed all their leaves more or less affected, and shed them continuously throughout the season. He stated that when defoliation was most severe the young branches of the season also had fallen off. This latter observation confirms that made by GÜSSOW in Canada. The writer has seldom seen so severe an infection as either of these, although in some localities the disease is severe enough each year to cause an incessant dropping of leaves throughout the summer and fall, which is a far from desirable characteristic in a lawn and avenue tree like *U. americana*.

Symptoms

The disease makes its appearance early in the spring, the amount of primary infection apparently being dependent to a considerable degree on the weather conditions, as it is much worse on the same tree in some years than in others. Clinton expressed the opinion that the only infection which occurred was the primary spring infection, and that there was no further spread during the summer. The fact that no conidial or summer stage had ever been found connected with the disease, and also his observation of trees which shed all their leaves early in the season and which later produced a new crop of foliage entirely free from spots, would tend to support this conclusion. The absence of the disease on the new crop of leaves, however, might have been due to weather conditions which were not favorable to the spread of the organism at that time. In any case, the writer has found a conidial stage constantly associated with the disease in every specimen examined, and the connection between the two stages will be clearly shown later. Observations show also that the primary infection is confined almost exclusively to the lowest leaves, and that it is much more abundant on the young seedlings, whose leaves are naturally closer to the ground, and to the ascospores which are the source of this early infection. Moreover, it is only on these young seedlings that twig and petiole infection has been observed, although there it is often quite severe, killing off the entire new growth.

The first evidence of the disease is a small whitish or yellowish fleck or blotch on the upper side of the leaf shortly after it has unfolded. This spot increases in size, and soon a number of small black specks begin to appear within the whitened area. As these enlarge they sometimes coalesce to form a single, coal black, stroma-like, subcuticular structure which is quite irregular in outline and varies from 0.5 to 2 or 3 mm. in diameter. As a rule, however, the individual stromata remain separate, when they appear to be somewhat concentrically arranged, forming a distinct spot, in most cases surrounded by a narrow band of whitish dead tissue as shown in fig. 12. Occasionally the black stroma, or the group of separate stromata, so closely grouped together as to seem to the naked eye to be a single one, may cover the entire discolored

area, without a border of whitish or lighter colored dead tissue. In this case it appears almost like a tar spot on the normal green leaf tissue, and reminds one of some of the species of *Rhytisma*. Later in the season the cuticle which covers the stroma wears away and gives the spot an ashen appearance, which is most pronounced near the edge. These black spots may be so numerous as to practically cover the entire upper surface of the leaf.

In addition to these black stromata, and much more prominent in the early stages of infection, although the reverse is the case later in the season, are the pustules of the conidial stage. They are quite abundant and conspicuous in the early spring, and it is hard to understand how they can have been overlooked for so long a time. They are subcuticular, irregular in outline, and dark, owing to the cuticle which is stained by the fungus, and which splits irregularly to allow the dispersal of the spores, which are extruded in small white masses. The pustules formed earliest seem to have but little or no stromatic base, although those formed later in the summer are almost invariably situated on a distinct stroma, which they may or may not entirely cover. This conidial stage will be discussed more in detail later.

Development of stromata

Beneath each one of the small, black, subcuticular stromata, as represented in fig. 13, early in its development, beginning about the latter part of May, there commences the development of the young perithecium of the causative fungus. The stroma now becomes somewhat looser in structure near its central region, beneath which the perithecium is to be formed. The normal cells of which the stromatic hyphae are made up are short, approximately isodiametrical (fig. 16), and contain comparatively little protoplasm, which little soon disappears, except in the basal layer of cells, and in those which are actively engaged in extending the edges of the stroma. They are more or less olivaceous to dilute brown in color, the depth of the hue depending on the age of the cell, but the very dark appearance of the stroma is due principally to a dark coloring matter which is not present in the cell wall to any extent, but seems to be excreted by the cells of the fungus

and deposited between their walls. A similar excretion of coloring matter was noted by KLEBAHN (22) in working with *Gnomonia veneta* (Sacc. and Speg.) Kleb. Within the looser portion of the stroma are to be found in this stage of its development other hyphae, which are very thin-walled, entirely filled with a very dense protoplasm, and have comparatively few septa. They stain pink or red with Pianeze IIIb stain (41), as do the other hyphae which enter into the formation of the young perithecium, but much more intensely. The ordinary stromatic elements, which have become comparatively inactive, take a green color with this stain. These deeply staining active hyphae ramify through the lower, looser portion of the stroma, a number of them turning upward near the center and breaking through to the outside, extending above the leaf surface as shown in fig. 16.

ASCOGONIUM

Immediately beneath this portion of the stroma there grows downward into the leaf tissue, between the epidermal cells and between the cells of the upper palisade tier (usually to a point near the lower edge of that layer), one of these hyphae which has become slightly larger in diameter. For convenience this hypha may be termed an "infection thread" or "suspensor," since it is the first of the fungal hyphae to invade the tissue of the host beneath the epidermal layer, and since in the early stages of its development the young perithecium gives the appearance of being suspended from the subcuticular stroma above by means of it. This hypha is accompanied in its growth downward into the host tissue by a number of other hyphae, consisting of short isodiametrical cells, which arise from the basal layers of the stroma and contain comparatively little protoplasm. They form a sheath for the broader, more deeply staining hypha, which for convenience only has been designated as an infection thread or suspensor. After growing to a point about midway down in the palisade layer, this cuts off a number of cells at its extreme end (fig. 16), usually three or four, which coil somewhat in the form of a spiral. Each one of these cells contains two or more nuclei, while the cells of the hyphae which constitute the sheath are uninucleate. These hyphae

meanwhile have continued their growth, dividing in such a manner as to produce a larger number of chains of cells which arrange themselves spirally about the central coil and form what is to become the wall of the perithecium.

This coiled structure is the ascogonium or "Woronin's hypha," described by various workers in a considerable number of Ascomycetes. I do not consider the hypha connecting it with the stroma above in any way analogous to a trichogyne, however, but rather as being similar to and corresponding to the hypha described by Miss DAWSON (**14**) as leading from the stroma beneath and giving rise to "Woronin's hypha" in *Poronia punctata*. The apparent differences between the two cases are that in *Poronia* the perithecium is formed in the upper part of the stroma, and the hypha which gives rise to the ascogonial coil comes up from below and does not leave the stroma; while in *Gnomonia ulmea* the perithecium is formed beneath the stroma in the tissue of the host, which renders it necessary for the thread which is to give rise to the ascogonium to leave the stroma and grow downward into the leaf tissue. In each case the hypha enters the perithecial primordium at a point which is finally located in the basal portion of the mature perithecium. In *Poronia*, however, after coiling to form the ascogonium, it continues to grow on beyond the perithecium to the outer surface of the stroma as a somewhat narrower thread, which reminds one of the trichogyne of *Collema*, as described by BACHMAN (**3**), of *Physcia* by DARBISHIRE (**11**), and of *Polystigma* by FRANK (**18**) and FISCH (**17**), but not by BLACKMAN and WELLSFORD (**4**). This "trichogyne" was not present in *Gnomonia ulmea*.

BROOKS (**6**), in working with *Gnomonia erythrostroma* (Auers.) Kleb., found an ascogonium similar to the one described for *G. ulmea*, and also certain structures which he called trichogynes. He was able to trace a connection between these hyphae and the peripheral layers of the young perithecium only, never with the ascogonium itself. These peripheral layers would correspond in fig. 16 to the sheathing hyphae *a*. Since more than one trichogyne passed through a single stoma in the case in which he was working, BROOKS concluded that more than one series of trichogynes was

connected with a single ascogonial coil. In *G. ulmea* also, as previously stated, one finds (fig. 16) certain hyphae which pass out through the upper leaf surface in a quite similar manner, although not through a stoma in this case, since stomata are absent on the upper surface of an elm leaf. In this case, however, there is no possibility of their being mistaken for anything else than vegetative hyphae. It is quite likely that those of *G. erythrostroma* are of a similar nature. BLACKMAN and WELLSFORD described in *Polystigma rubrum* trichogynes similar to those of BROOKS, but on account of an inability to trace a direct connection with the ascogonium, concluded that they were merely vegetative. In earlier papers FISCH (**17**) and FRANK (**18**) had both described and figured such connections and had designated the hyphae as true trichogynes. Although BROOKS continued to call the projecting hyphae in *G. erythrostroma* trichogynes, and although he found both ascogonia and spermatia present, he concluded that the trichogynes were no longer functional, and that fertilization did not actually occur through their agency. He suggested as a present function for them that they might serve as respiratory channels for the fungal hyphae within the leaf, where the assimilatory processes must necessarily have been considerably curtailed by the dying of the tissue. Such a function would also give reason for the existence of similar hyphae in *G. ulmea*, especially since the presence of the black stroma would tend even more to impair the respiratory processes in the host tissue beneath it.

The ascogonium in the young perithecium of *G. ulmea* soon begins to break up into segments, each cell becoming separated from the others. BROWN (**7**) noticed a similar segmentation of the ascogonium of *Xylaria tentaculata*, as did also Miss DAWSON in *Poronia*. They found that those segments gave rise to the ascogenous hyphae in the fungi with which they were working, but I have been unable to ascertain this fact with certainty in *G. ulmea* with the material at hand. It is almost a certainty, however, that this is the case here also, since the segments of the ascogonial coil can be distinguished near the base of the perithecium until after the asci have commenced their development.

FURTHER DEVELOPMENT OF PERITHECIUM

In the further development of the young perithecium all sign of the connection with the subcutaneous stroma soon disappears, as is shown in fig. 2, which is a slightly older stage. The structure has increased in size, chiefly by the enlargement of the portion which is later to become the perithecial cavity, but which is now filled with a dense pseudoparenchyma. The wall has also increased somewhat in thickness by the formation of new layers on the inside. As yet there is no sign of a beak or ostiole, although the wall cells on the lower side of the perithecium, opposite the stroma, are somewhat denser in protoplasmic contents, as is shown by the slightly darker color. Fig. 8 shows a still later stage of development in which the perithecium has practically doubled in size, since the two figures are of the same degree of enlargement. The central area has enlarged and the wall become still thicker. The darkly stained portion is composed of young asci which are not yet clearly differentiated. On account of the nature of the material, the leaves showing this stage of development having first been collected and dried and later softened with lactophenol, as well as on account of the very small size of the nuclei, the cytological and other minute details of this development could not be accurately determined. The main portion of the perithecial cavity is entirely filled with a very fine pseudoparenchymatous material, which when crushed or teased out appears merely granular in structure, with some slight evidence of anastomosing hyphae. In the original description of the fungus, SCHWEINITZ mentions the granular nature of the perithecial contents. The beak or rostrum and the ostiole are here seen in the earliest stages of their development. The same group of more deeply staining wall cells, mentioned in connection with fig. 2, is still evident, but has increased in size to form a sort of plug of tissue, which by its growth forces the outer layers of the perithecial wall outward and downward on the lower side to form the outer wall of the beak. As the multiplication of these actively dividing cells continues, their long axis changes from horizontal, as at first, to a direction parallel to that in which the beak is being developed. The cells nearest the center of this elongating beak separate in their continued growth, leaving a

channel throughout its entire length which becomes the ostiole. This channel is lined with periphyses or hairlike structures which are hyphal outgrowths of the inner or lining layer of cells. These periphyses all point in a direction outward from the perithecial cavity, and so form a one-way passage from the spore bearing portion to the outside of the leaf. As the development of the beak nears completion, each layer of cells, whose increase has brought about its elongation, produces at its lower end one or more of these periphyses to each cell, so that the lower end or outer opening of the ostiole is surrounded by a considerable brush of them. These later stages of the development of the ostiole are seen in fig. 1, which shows two perithecia in an almost mature condition. The beaks are slightly longer than normal at this stage of maturity, but in all other respects the perithecia are typical. No further elongation of the beaks occurs until the ascospores are fully mature and ready to be discharged, sometime in the early spring, at which time they again begin growth and continue until they have just broken through the lower epidermis. In this stage, which is the condition in which they pass the winter, the lower end of the beak is still within the leaf tissue and merely pushes out the lower epidermis in the form of a hump or tubercle. In the spring, when they have just broken through, these beaks, although short, are quite conspicuous on account of their fresh dark brown or almost black color.

The asci in the figure last referred to are not yet mature, and it will be seen that the pseudoparenchyma is still present. This tissue is composed of small hyaline cells, filled with a very dense granular protoplasm, and with very thin walls; in fact, the walls are little more than membranes. It occupies the entire central region before the development of the asci, which grow out into it, and apparently it is used up by the asci in their growth, as no crowding of the tissue is apparent ahead of them. Such an interascicular pseudoparenchyma has been described by STEVENS (35), who used it as the basis for the formation of a new genus, *Desmotascus*. He considered it an instance of delayed dissolution of the pseudoparenchymatous central region of the developing perithecium to form the central cavity, and suggested that, since this

structure was not clearly seen without good thin microtome sections, the same thing may exist in other perithecia and have been overlooked because the microtome was not used. The finding of such a structure in *Gnomonia ulmea* would tend to support such a hypothesis. REDDICK (**29**), working with *Guignardia bidwellii*, found that when the first asci were developing not nearly all the pseudoparenchyma was gone, and that, when crowded together by the growth and expansion of two asci, it gave the impression that paraphyses were present. He also expressed the opinion that these cells were absorbed by the growing asci. This case differs from that found in *Gnomonia ulmea* and also from that described by STEVENS in *Desmotascus* only in that the pseudoparenchymatous cells in the latter two fungi never appear to be crowded by the invasion of the asci.

The asci originate from the basal portion of the perithecial cavity, and also from the sides to a point about halfway to the top. The perithecial walls are composed of from 10 to 12 rows of cells (fig. 1), the outer one or two layers of which have assumed a bright golden brown color. It is at about the time when the ostiole is being developed that this coloration of the wall begins. Until that time the wall has been entirely hyaline. From this time on, as the perithecia age, this color becomes constantly darker, until about midwinter, when it is almost black. The outer surface of the perithecium is smooth, and there are no loose hyphae connecting it with the leaf tissue in which it is borne.

When mature the perithecia are nearly spherical or usually somewhat wider than deep. They vary considerably in size, but average about 250–300 μ in diameter and 150–200 μ in depth. The ostiole is usually about 100 μ long and 75 μ wide, but may reach a considerably greater length. The size of the perithecium is so great that the upper epidermis is elevated in the form of small tubercles, and the beaks push out the lower epidermis in the same manner, before they break through it. They do not extend any distance beyond the outer surface of the lower epidermis, as do so many of the species of *Gnomonia*, but merely reach through it. When the over-wintered leaves have been soaked in water, the perithecia may be picked out with the point of a sharp scalpel, and

on account of the absence of any hyphae connecting them with the leaf tissue, they leave a smooth cavity or locule in the leaf.

Asci and ascospores

In mature perithecia the asci are very much confused in their arrangement, owing to the fact that the older ones are broken loose from their attachment and pushed toward the top of the perithecial cavity by the younger ones. There are no paraphyses. The asci are oblong-cylindrical or somewhat club-shaped in form, and have a short stalk at the base which may be either straight or bent toward one side. The wall is hyaline, thin below, but thickened in the upper half (fig. 19), and does not color with iodine. At the upper end of the ascus is a pore surrounded by a ring of thickened tissue which is strongly refractive toward light. In optical section as seen from the side this ring presents the appearance of two small spheres arranged side by side in the apex of the ascus. The asci measure 45–55×9–11 μ. The spores are very characteristic also. They are hyaline, elongate-elliptical, or obovate-oblong, and have a septum near the lower end, thus becoming unequally two-celled. They are eight in number, subbiseriate, and measure 8–10×3–3.5 μ. The small cell at the lower end of the spore averages about 2 μ both in length and breadth. There is a slight constriction at the septum. Some epiplasm is present in the mature ascus along with the spores.

Expulsion and germination of ascospores

As previously stated, the asci in a mature perithecium become loosened from their attachment at the base and crowded toward the apex of the perithecial cavity in a somewhat disordered mass. In the process of expulsion of ascospores an entire ascus enters the lower part of the ostiole and is held in place by the periphyses until the pressure produced by the absorption of water, which must be present to allow the ascospores to be discharged, becomes sufficient to bring about the discharge of the spores. These pass outward through the periphysis-lined ostiolar channel to the surface of the ostiole, where they are expelled with some force, and under natural conditions are evidently dispersed by currents of air. Early in March leaves were found which had passed the

winter in the open under natural conditions, on which occurred perithecia in such a stage of development as to expel ascospores within two days after being brought into the laboratory. It was found that spore expulsion was very slow and limited or did not occur at all when the leaves were kept too moist or when maintained in a saturated atmosphere, such as occurs when they are placed on moistened filter or blotting paper in a closed Petri dish. When the lid of the dish is removed, however, and the leaves are alternately allowed to become dry and again moistened by adding water to the filter paper beneath them, the spores are expelled in considerable quantities. If they are then caught on a glass slide, either dry or coated with a thin film of egg albumin, glycerine, or some such adhesive, it is found that the spores are deposited in clusters or groups of eight. Later, as a very large number of spores are discharged from a single ostiole, this grouping of course is not apparent. The best method for catching the expelled spores was that used by ANDERSON and RANKIN (1) in working with *Endothia parasitica*, as described previously. The glass slide was suspended by means of match sticks fastened to it near the ends, thus bringing it 3 or 4 mm. above the opening of the ostiole.

KLEBAHN (27) has shown that this method of spore expulsion is general to *Gnomonia* and to many other fungi which have *Gnomonia*-like, beaked ostioles. The expulsion of the asci into the neck of the ostiole appears largely due to the swelling pressure of the ascus. When dry, the ascus with its contained spores occupies considerably smaller space than after it has been moistened with water. Many workers have maintained that ascospores are ordinarily liberated one at a time, and such may be the case here, since I have been unable to observe the actual act of expulsion of the spores from the ascus, but the clusters of the spores intercepted on a glass slide suspended above the opening of the ostiole are always in groups of eight, and give the impression of having been expelled in a group, as was found by ANDERSON and RANKIN to occur in *Endothia parasitica*.

Many attempts have been made to germinate the ascospores of *Gnomonia ulmea* under various conditions, and on a number of different nutrient media, ranging from distilled water, tap water,

extract of dried elm leaves, and sugar solutions, to solid media such as the agars of cornmeal, bean, potato, Brazil nut, onion, elm leaf, and plain washed agar. In distilled or tap water the spores swelled considerably, especially the larger cell, and sometimes a spore would give the appearance of being on the point of sending out a germ tube from the side of the larger cell, but this never occurred. This is in accordance with the results obtained by KLEBAHN (**27**) in *Gnomonia alniella* and *Gnomoniella tubiformis*, which he was not able to grow in culture, but is contrary to his results with *Gnomonia platani* and *G. leptostyla*, both of which grew well on nutrient media, the latter even producing the perithecial stage in such cultures. It would seem that the ascospores of *Gnomonia ulmea*, as in *G. alniella* and *Gnomoniella tubiformis*, require the stimulation given by the green leaf of the host plant itself in order to induce germination. WOLF (**42**) found that this was the case in *Diplocarpon rosae*, the ascospores of which would not even germinate in a drop of water in which a portion of a green leaf of the host had been placed, but must be placed in a drop of water directly on the living leaf itself. This assumption was later confirmed by experimentation. Toward the middle of March a number of twigs were cut from an elm and placed in the greenhouse with their cut ends immersed in water. In about three weeks the buds on these twigs unfolded. A number of the young leaves were removed and placed in a moist chamber with their surfaces in contact with a slide on which a large number of the expelled spores of *Gnomonia ulmea* had been intercepted as previously described. Intimate contact was secured by moistening the surface of the slide to which the spores adhered with a drop of water. By removing the leaf it was possible to examine the spores on the slide by means of a microscope, but never was one of them found to have germinated. Later, when the leaves on the trees outside the greenhouse had begun to unfold, the same experiment was attempted again, and in twelve hours it was found that a considerable number of the spores in contact with the leaves had germinated. This led to an examination of the tree from which the leaves used in the first experiment had been obtained, and it was ascertained to be an English elm, *Ulmus campestris*.

This led to a further attempt to germinate the spores on the leaves of both the English and the Scotch elm, *U. glabra*, but without success in either case. A considerable percentage of germination, however, was always obtained with *U. americana*. These experiments would seem to indicate that the germination of the ascospores of *Gnomonia ulmea* is dependent on a special stimulus of some sort exerted by the leaves of susceptible species of *Ulmus*, but which is absent in the leaves of other species of the same genus, just as it is absent in tap or distilled water, and the various liquid and solid nutrient media in which attempts were made to grow the fungus.

At the end of twelve hours of contact with the leaf of the American elm under suitable moisture conditions, as previously stated, the spores were found in various stages of germination. Wherever two spores lay in contact with each other and also with the leaf, there was noted a brown coloring matter deposited between them. This coloring matter is similar to that previously mentioned as being deposited between the hyphae of the stroma and on the lower side of the cuticle. The germ tube usually arises from the large cell of the spore only, as shown by fig. 20, although in a very few instances the small cell also may send out one. Germination apparently can occur from any point in the spore, although usually the germ tube makes its exit from the side of the large cell. One can tell where the germ tube is going to form even before any swelling occurs by the excretion of the brown coloring matter on the outside of the spore wall at that point. As the tube grows, the coloring substance is deposited along its entire length, except at the extreme apex, but in considerably greater density at the point where it leaves the spore. The substance is present in greater abundance also wherever two germ tubes touch or cross each other.

Inoculation with ascospores

On April 6 a number of abscissed twigs of *Ulmus campestris*, whose leaves had unfolded in the greenhouse, were inoculated with the ascopores of *Gnomonia ulmea*. Twelve twigs were used, six being sprayed by means of an atomizer with a suspension of spores, while six similar ones were sprayed with sterile distilled

water to serve as checks. Each set was kept under a bell jar, whose inner surface had been lined with moist filter paper, for a period of 42 hours, after which they were left in the normal atmosphere of the greenhouse. A like number of twigs of *U. americana*, whose leaves had unfolded normally outside the greenhouse, were treated in a similar manner. As was to be expected from the failure to secure germination of the ascospores on the leaves of the English elm, no infection occurred on that host. On April 25, however, or after a period of about three weeks, eight leaves of the American elm were found to bear well defined spots quite characteristic of the early stages of *Gnomonia ulmea*. Two of these leaves bore three spots each, another one two, and the other six had only a single one on each. These spots showed well developed pustules of the conidial stage, which is to be described later. In addition to these well defined spots a number of leaves showed small whitish flecks or blotches, thereby indicating that if the experiment had been allowed to continue for a longer period the percentage of infection would have been higher.

Observations on over-wintering

A number of observations have been made on the over-wintering of the fungus on elm leaves under various conditions, and some attempts have been made to hasten its development by placing the leaves under various controlled conditions. Leaves on which the spots occurred were brought into the laboratory, both before and after they had been severely frosted, and some were immersed in water, both at room temperature and in the refrigerator. Others were placed in a moist chamber suspended over water, both in the laboratory and refrigerator, and others were placed in each of these places under their normal conditions of humidity. Still others were suspended over calcium chloride in each of these temperatures in order to assure a dry atmosphere. It was found that no further development occurred in the leaves which were immersed in water, and that the fungus soon died, the perithecia becoming mere empty husks. This was confirmed by comparison with leaves which had wintered normally outside the laboratory. On leaves which had been buried slightly in the soil or were in close

contact with the soil underneath a layer of other leaves, the perithecia were found in early spring to be in approximately the same condition. No further development of the fungus occurred on the leaves either suspended above the calcium chloride or in the normal humidity conditions of the laboratory or of the refrigerator. The fungus in the leaves which had been suspended above water in a moist chamber, however, did continue its development, and by midwinter a few perithecia were found in which the spores were apparently practically mature. In most, and finally in all cases, however, numerous saprophytes developed in such abundance that the *Gnomonia* fungus was overgrown and destroyed before the spores could mature. Other leaves from outdoors were brought into the laboratory at various times throughout the winter and placed in moist chambers, but the same development of extraneous saprophytes soon stopped the observations. In a number of instances observed the *Gnomonia*, apparently in an effort to counteract and overcome the encroachments of the more rapidly developing saprophytic fungi, began to grow vegetatively, and the entire perithecial cavity as well as the ostiolar canal became filled with a mass of interlaced and anastomosed hyphae, so compacted together that under pressure the perithecial wall would break away, but the interior mass would tend to retain its spherical shape. This tissue later died and disintegrated, however, leaving the empty husk of the perithecium. Among the saprophytes which hindered observations a number of forms were invariably present. They were, in the main, *Cephalothecium roseum*, *Phycomyces nitens*, several species of *Penicillium* and *Aspergillus*, an *Alternaria*, a *Pleospora*, a *Crytostyctis*, and a Myxomycete.

Various observations also were made on leaves wintered outside the laboratory. Some leaves were placed on shelves of a wire cage, others were placed on the ground and covered with other leaves and soil, while still others were wrapped in cheesecloth and placed on the surface of the ground. In the leaves placed on the shelves and on the surface of the ground the fungus was found to mature more rapidly than on those leaves covered with other leaves and soil, and a very few perithecia were found on such, which

contained some spores apparently almost mature as early as the middle of February. On only one leaf, however, were any of the perithecia at that time mature enough to expel spores. This leaf was on the shelf of the wire cage, which was placed directly against the south wall of the greenhouse, and was exposed both to the direct rays of the sun and also to the heat rays radiated from the cement wall. In most cases at that time the asci were somewhat more developed than when observed in the fall, but the spores were not yet differentiated. The normal development during the winter, therefore, seemed to be very slow. In leaves which were in especially damp situations, as those buried in the soil or those in intimate contact with the soil under a cover of other leaves, most of the perithecia were found to be dead and disintegrated. In general, it seemed that leaves neither in too exposed nor too moist a situation, as for instance those toward the middle of a pile of leaves, showed the greatest development of the fungus late in winter and early in the spring.

Conidial stage

In every specimen examined in which the ascigerous stage of *Gnomonia ulmea* occurred, I have found constantly associated with it an imperfect or conidial form. This stage was found present from early spring until late fall on every leaf collected, and also on all exsiccati material examined, even the Schweinitzian type specimen previously mentioned. I have examined all available published exsiccati specimens of *Gnomonia ulmea*, as well as more than 100 other specimens obtained for purposes of comparison from various educational institutions and private individuals, including several from the Royal Botanical Gardens, Kew, England, and the herbarium of the University of Geneva, Geneva, Switzerland. The published exsiccati specimens examined are as follows: Ravenel Fung. Amer. Exsic. no. 752; Ravenel Fung. Carol., Fasc. II, no. 63; Ellis and Everhart Fung. Col. nos. 239, 2928, and 3422; Seymour and Earle Econ. Fung. nos. 155a and 155b; Ellis N. Am. Fung. no. 1347; Brenckle Fung. Dakotensis no. 329; Rabenhorst-Winter Fung. Eur. nos. 3661a and 3661b; and von Thümen Myc. Univ. no. 1155.

The conidial layer develops on the stroma which is found on the upper surface of the leaf above the base of the young perithecium (fig. 14). It may cover only a portion of the stroma, and there may be two or even more of them on a single one of the stromata. Again, a stroma may develop, to all appearances identical with those formed above the bases of the young perithecia, but the perithecium be lacking. In this case the conidial pustule invariably covers the entire surface of the stroma. Moreover, in the case of the first pustules formed in the spring, there is usually little or no stromatic base present.

The conidial pustules are quite irregular in outline (fig. 18), although usually approaching a somewhat circular shape. Unless two or more of them coalesce, which frequently, in fact usually, happens, they may become considerably elongated and variously lobed. The size also varies to a considerable extent, due to the coalescing of a number of different pustules. The average size is about 0.5 mm. in diameter, although they may be considerably smaller, and have been seen as large as 0.8 mm. The upper layers of cells of the subcuticular stroma elongate in a direction at right angles to the surface of the leaf and form the conidiophores. These press closely against the cuticle and lift it up somewhat in the course of their development. At the same time they give off a brown coloring matter which is deposited on the inner or lower side of the cuticle, which itself remains colorless. This coloring substance is deposited more deeply at the points between the conidiophores than directly above them, so that the darkened cuticle presents a somewhat reticulate or netted marking, and on casual observation appears to be composed of fungal tissue. This gives the impression that the conidial pustule is of the nature of a dimidiate pycnidium. Closer observation, however, shows that no fungal hyphae enter into this covering layer, and the structure consequently is found to be melanconiaceous in character. The deposition of coloring matter on the cuticular coverings of such acervuli has been noted by KLEBAHN in connection with the conidial stages of *Gnomonia padicola* (**23**), *G. leptostroma* (**22**), and *Gnomoniella tubiformis* (**24**). As previously stated, the same substance is deposited between the cells of the hyphae which make up the

stroma, and which now have become the cells of the hymenial layer from which the conidiophores arise. It is also frequently found deposited between the cells of the epidermis immediately beneath the stroma.

These epidermal cells are not changed to any considerable extent except for crystalline substances occasionally found deposited in them. The fungal hyphae grow down between them and crowd them apart somewhat, but they do not lose their arrangement as a definite layer. The hyphae of the fungus do not penetrate the cells of the host. The conidiophores are crowded together into a very compact layer, and are 8–12 μ long by 1.5–2.5 μ thick. They are without septa, except for an occasional one near the base, and terminate in a threadlike projection on which the spores are borne. The conidia are elongate-oblong or cylindric, bacillar, pointed at one or both ends, straight or sometimes slightly curved, one-celled, hyaline, and measure 5–6×1–1.5 μ (fig. 15) in a dry state, but 8–10×2–2.5 μ when freshly collected.

Since there is no fungal covering to the conidial layer, the fungus falls into the family Melanconiaceae, and its other characters indicate beyond a doubt that it is a member of the genus *Gloeosporium*. It seems to be quite characteristic of *Gnomonia* to have a conidial stage which is melanconiaceous in character. *Gnomonia padicola* has as an imperfect stage *Asteroma Padi*, but according to KLEBAHN (**26**) no true pycnidium is formed. *Gloeosporium nervisequum* is connected with *Gnomonia veneta*, *Marssonina Juglandis* with *G. leptostyla*, *Gloeosporium quercinum* with *G. quercina*, *Gloeosporium Caryae* with *G. Caryae*, *Gloeosporium Tiliae* with *G. Tiliae*, and *Leptothyrium alneum* with *Gnomoniella tubiformis*. KLEBAHN (**25**) has shown also in connection with *Leptothyrium alneum* that no true pycnidial covering is formed, and that consequently it is melanconiaceous in structure. SACCARDO (**30**) also remarks concerning this species "(perithecio) subinde tamen spurio et ex epidermide mutata et atrata formato."

The genus *Gnomonia* contains a number of species which form no conidial stage, or at least whose conidial stage has not yet been discovered. In so far, however, as the conidial stages have been established in the genus, it is evident that they conform to a

more or less close resemblance to *Gloeosporium*. The *Leptothyrium* of *Gnomoniella tubiformis* is scarcely to be distinguished from a *Gloeosporium; Asteroma* of *Gnomonia padicola* differs from it only in the production of superficial mycelium; and *Marssonina* of *Gnomonia leptostyla* only in its two-celled conidia.

Among the many fungous diseases occurring on the leaves of the elm, only a few have been found whose causative organisms are located in the Melanconiaceae. Three of these belong to the American flora, namely, *Goryneum tumoricolum* Peck, *Septogloeum profusum* (Ell. and Ev.) Sacc., and *Cylindrosporium ulmicolum* Ell. and Ev. I have not seen ELLIS and EVERHART'S specimen of *Cylindrosporium ulmicolum*, and it may be identical with *Phleospora Ulmi* (Fr.) Wallr., since the two descriptions appear very much alike. *Septogloeum profusum* has been reported as occurring on the leaves of *Ulmus alata* and *U. americana*, although it was originally described on *Corylus americana*. Two species of *Gloeosporium*, or rather one species and a variety of the same, have been described on the elm in Europe. One of these, *Gloeosporium inconspicuum* Cav., was described on *Ulmus americana* in Italy, but has never been reported in this country. It was distributed by BRIOSI and CAVARA in "Funghi parassiti" as no. 350. It causes large ochraceous spots on the upper side of the leaf, and has very small bacteriform spores, only 1–2 μ in length. A variety of this species, *Gloeosporium inconspicuum* Cav. var. *campestris* Dor. (15), has been described on *Ulmus campestris* in Russia. From the description this is quite similar in external appearance to the preceding species, but the spores and conidiophores are considerably larger, the spores measuring 3–6 (sometimes 9) $\times$ 1–2 μ. The fungus described as occurring on *Ulmus americana* and other species of elm in America in connection with *Gnomonia ulmea* does not agree in any particular with any of these, and therefore I propose for it the name *Gloeosporium ulmeum*, with the following formal description.

Gloeosporium ulmeum, sp. nov.—Acervuli somewhat gregarious, often confluent, borne on black stromata, usually over the base of the developing perithecium of *Gnomonia ulmea*, covered by the darkened cuticle, which later splits and cracks irregularly

and finally breaks away entirely, subrotund or irregular, averaging 500 μ in diameter, but often as large as 800 μ, epiphyllous, very rarely hypophyllous; conidiophores cylindrical, crowded, occasionally with a septum near the base, 8–12×1.5–2 μ, terminating in a threadlike projection on which the spores are borne; conidia elongate-oblong or cylindric, bacillar, pointed at one or both ends, straight or very slightly curved, hyaline, one-celled, 5–6×1–1.5 μ in a dry condition or 8–10×2–2.5 μ when freshly collected, and extruded in small white masses.

Habitat on the living leaves of *Ulmus americana*, *U. fulva*, *U. alata*, *U. racemosa*, and *U. crassifolia*. Common. Conidial stage of *Gnomonia ulmea* (Schw.) Thüm. and constantly associated with it, the two stages occurring concurrently on the same leaf and spot. Type specimen on *U. americana*, collected at Urbana, Illinois, August 1919, and deposited in the herbarium of the University of Illinois. Differs from *Gloeosporium inconspicuum* Cav. in the very different appearance of the spots and in the larger size of its spores, and from *Gloeosporium inconspicuum* Cav. var. *campestris* Dor. in the character of the spots.

Inoculations with conidia

On April 25 a number of leaves of the American elm were placed in a moist chamber lined with filter paper, and at a definite point on each was placed a drop of distilled water containing a considerable number of spores of *Gloeosporium ulmeum*, the conidial stage of *Gnomonia ulmea*. On June 2 most of these spots were lighter in color than the remainder of the leaf, and on June 5 a few of them showed distinct conidial pustules entirely characteristic of the fungus with which the leaf had been inoculated. On the same day on which this experiment was started a number of leaves of a seedling elm, quite healthy in appearance and growing naturally in the open, were sprayed with a suspension of the same spores in distilled water by means of an atomizer, and the entire twig was inserted into an Ehrlenmeyer flask. The mouth of the flask was closed by means of a split cork in which a channel had been hollowed to fit about the twig. The flask was supported by means of props in such a manner that the twig remained in its proper position. On June 5 the entire new growth of the twig was found to be covered with a practically continuous layer of pustules of *Gloeosporium ulmeum*, all of which were extruding

spores copiously. Not only were the leaves badly infected, but also the petioles and the stem itself.

These experiments, together with the production of the conidial stage on the leaves of the American elm inoculated with the ascospores of *Gnomonia ulmea*, prove conclusively that the two forms are merely stages of the same fungus. The enormous number of spores produced by the conidial stage, as well as the fact that infection secured from inoculations with such spores was much more pronounced and occurred in a somewhat shorter period of time than from inoculation with ascospores, would seem to indicate that the *Cloeosporium* stage is the chief agency through which widespread dissemination occurs in the spring and early summer.

Another Gloeosporium on elm

While working with this fungus, a single tree in a nursery at Oconomowoc, Wisconsin, was found on which the leaf spots were quite different in external appearance from those on the surrounding trees, most of which were abundantly spotted with the *Gnomonia* disease, although the trees were of the same species and had apparently been planted at the same time. Fig. 9 shows a leaf from this collection. The leaf spot is raised considerably more than is the case in the preceding species, giving the portion of the leaf on which it occurs a crumpled appearance where the spot becomes large, and is confined quite closely to the leaf veins, along which it spreads, often extending the entire distance from the midrib to the edge of the leaf, thus forming elongated streaks. The leaf veins also become browned for some distance beyond the spots, although the remainder of the leaf is a normal green. The spots present a gray salt-and-pepper aspect, due to the whitened epidermis over which the black conidial pustules are thickly scattered. The whitened appearance is due also to the disappearance of the contents of the epidermal cells and from the cells of the palisade layer immediately beneath them. This disappearance of cell contents is much more pronounced than in the *Gnomonia ulmea* spot.

The acervuli are very numerous in a single spot and are quite commonly confluent. They are orbicular to oblong in shape, very irregular in outline, and are covered by the darkened cuticle

which persists for a long time, finally cracking and breaking irregularly to allow the dispersal of the spores. They average 800 μ in diameter. The hymenial layer is pseudoparenchymatous, composed of practically colorless cells which are almost isodiametrical in shape. This layer may be even thicker than that described for *Gloeosporium ulmeum*, although it presents an entirely different appearance, and on account of the absence of color does not at all suggest a stromatic base. The layer appears even thicker than it really is on account of the absence of all color from the epidermal cells, which have become entirely filled with small colorless crystals. This is true to a less extent of the adjacent layers of palisade tissue. The conidiophores are closely packed together, and are quite similar to those of *Gloeosporium ulmeum* except for their larger measurements, being 10–15×2–3 μ. They are not as darkly colored as are those of the preceding species, although they are not entirely hyaline. The apex is rather blunt, and the conidiophore terminates rather abruptly in a sterigma-like projection on which the spore is borne. Occasionally two of these sterigma-like processes occur on a single conidiophore. The conidia are much larger, especially in width, and vary considerably in form, from oblong-cylindric to ovate, elliptical, and even pyriform. They measure 8–10×3–3.5 μ (fig. 17), are one-celled, rounded at both ends, straight, and hyaline. In no case was the perithecium of *Gnomonia* or any similar fungus found associated with this spot. I consider it entirely distinct from the conidial stage of *Gnomonia ulmea*, and propose for the fungus the following name and description.

Gloeosporium ulmicolum, sp. nov.—Spots epiphyllous, raised, gray on account of the black acervuli thickly scattered over the whitened epidermal cells, elongated, following the leaf veins, often extending the entire length of the secondary veins which have become browned far beyond the limits of the spot; acervuli epiphyllous, gregarious, subcutaneous, covered by the persistent darkened cuticle which finally ruptures irregularly to allow the dispersal of the spores, averaging 800 μ in diameter, irregular in outline but usually elongated suborbicular; conidiophores in a closely packed layer, dilute-brown, cylindrical, usually nonseptate

but occasionally with a septum near the base, seated on a pseudoparenchymatous hymenial base which is colorless, 10–15×2–3 μ, terminating rather abruptly at the apex in a sterigma-like projection on which the spores are borne; conidia hyaline, one-celled, straight, rounded at both ends, oblong-cylindrical, ovate, elliptical, or even pyriform, 8–10×3–3.5 μ.

Habitat on living leaves of *Ulmus americana*. Oconomowoc, Wisconsin, August 22, 1919. Type specimen deposited in the herbarium of the University of Illinois. This species differs from *Gloeosporium ulmeum* in the shape and appearance of the spots, in the fact that it is not associated with a perithecial stage as that fungus constantly is, in the absence of a black basal stroma, and in the larger spores. In external appearance the two forms are quite distinct. It differs also from *Gloeosporium inconspicuum* Cav. and *G. inconspicuum* Cav. var. *campestris* Dor. in the character and appearance of the spot and in the much larger spores.

Principal European leaf spot

SYSTREMMA ULMI (Schleich.) Thiess. and Syd.—The leaf spot of the elm occurring in Europe on *Ulmus campestris*, *U. effusa*, and *U. glabra* has a somewhat superficial resemblance to that produced in this country by *Gnomonia ulmea* (Schw.) Thüm. This may readily be seen by comparing fig. 6, which shows the European spot on a leaf of *Ulmus campestris*, with figs. 4 and 5, which are leaves of *U. americana* affected by the *Gnomonia*. The two diseases have been much confused in this country, and it has been quite common for American plant pathologists and mycologists to speak of the latter fungus under the name of the European organism. In examining specimens of the *Gnomonia* spot in various collections in this country, I have found it quite as often referred to in this manner as under its true name or synonyms. There are two references in literature to the occurrence of the disease caused by *Systremma Ulmi* in America, in addition to various others which are clearly due to a confusion of the two forms. One of these cases is in the report by TRELEASE (40) of the presence in Wisconsin of *Phyllachora Ulmi* Fuck., which name is a synonym of *Systremma Ulmi*. On examination of the specimen, which is in the museum of the Shaw Botanical Gardens at St. Louis, Missouri, it was found that the disease was the American form, caused by

Gnomonia ulmea. TRELEASE also reported the presence on the same leaf of *Septoria Ulmi* Fr., a synonym of *Phleospora Ulmi* (Fr.) Wallr., which at that time was thought to be the conidial stage of *Phyllachora Ulmi*, but I was unable to find any trace of it on the specimen examined. In material sent from the University of Geneva, Switzerland, I found another specimen, evidently from this same collection by TRELEASE and labeled in the same manner. It also was *Gnomonia ulmea*.

The second reference to the occurrence of *Systremma Ulmi* in this country is by ELLIS and EVERHART (**16**), who stated that a specimen of *Dothidella Ulmi* (Duv.) Wint., which name is merely another of the numerous synonyms under which the European organism is known, was sent to SCHWEINITZ by TORREY from New York. They added that they could not find any other references to this species being found in this country, and that they have seen no American specimens. I find in SACCARDO'S (**33**) *Sylloge Fungorum* in the description of *Sphaeria apertiuscula* Schw. on *Ulmus fulva*, collected by TORREY in New York, the statement added that the upper side of the leaf is covered with *Dothidea Ulmi*. This is evidently the specimen to which ELLIS and EVERHART were referring, as both the names used are synonyms of *Systremma Ulmi*. I have not seen this specimen, and there is a possibility that it is really a specimen of the European leaf spot, but it is hardly likely, especially since it has never been collected in this country since, nor has it ever been reported as occurring on *Ulmus fulva* at any other time, either previous to that collection or later.

I found in specimens sent from the Royal Botanical Gardens at Kew, England, among those labeled as belonging to the herbarium of BERKELEY, three specimens purporting to have been collected by DRUMMOND in arctic America. These were undoubtedly specimens of *Systremma Ulmi*, and, although the host was not named, the leaves possessed the somewhat three-lobed character peculiar to the Scotch elm, *U. glabra*. This is not native to America, and one would hardly expect to encounter an introduced species in the arctic regions. For these reasons I believe that these three specimens represent some European collection

which has in some manner accidentally become mixed with DRUMMOND'S arctic collections while they were in the process of being mounted at the museum. This seems all the more probable when it is noted that the handwriting on the labels is the same as that on a great many of the other specimens from the same museum. It would seem, therefore, quite probable that *Systremma Ulmi* does not occur at all in America. Although ELLIS and EVERHART place the causative organisms of the two diseases in the same genus, they express a caution against confusing the two, stating that although they have spores essentially the same they differ very markedly in other characteristics. In spite of the fact that the external appearances of the two spots seem quite similar to the casual observer, as soon as one sections them the very marked differences between the two fungi become apparent. Fig. 10 represents a section through the stroma of *Systremma Ulmi*. It will be seen that the black stroma, to which the external resemblance between the two forms is due, is in this case subepidermal, while in *Gnomonia ulmea* it is subcuticular only. In the *Systremma* the asci are produced in locules without true perithecial walls, which are imbedded in the stroma and open on the upper side of the leaf, while in *Gnomonia* the perithecia, truly sphaeriaceous in character, are located in the leaf tissue beneath the stroma and open on the under side of the leaf. *Gnomonia ulmea*, therefore, belongs to the Sphaeriales, while *Systremma Ulmi* belongs to an entirely different order, the Dothidiales. Although the asci and spores of the two differ but little in form, both are slightly larger in *Systremma* than in *Gnomonia*.

I have examined all available published exsiccati specimens of this fungus, as well as about 200 other specimens borrowed for purposes of examination and comparison from the Royal Botanical Gardens at Kew, and from the University of Geneva, and from a number of institutions and individuals in this country. The published exsiccati of this fungus examined were as follows: BERKELEY Brit. Fung. no. 192; VIZE Mic.-Fung. Brit. no. 277; COOKE Fung. Brit., Ser. I, no. 184; BRIOSI and CAVARA Fung. paras. no. 73; POLLACCI Fung. Longobardiae Exsic. no. 287; SACCARDO Myc. Ven. nos. 231 and 642; ROUMEGERE Fung. Sel. Exsic. nos. 466 and

5761; Fl. Gall. et Germ. Exsic. no. 1000; SCHLEICHER Crypt. Exsic. no. 73; HOLL, SCHMIDT, und KUNZE Deut. Schwamme no. 32; DESMAZIERES Crypt. Fr., Ser. I, no. 284; MONGIER et NESTLER Stirpes Crypt. no. 766; VON THÜMEN Fung. Austr. no. 499; VON THÜMEN Myc. Univ. no. 2064; FUCKEL Fung. Rhen. nos. 1013 and 2265; SYDOW Myc. Mart. no. 256; LUNDH. Fung. Hung. no. 374; RABENHORST Herb. Myc. no. 658; WESTEND. Herb. Crypt. no. 111; KRUEGER Fung. Sax. no. 1514; ERIKSSON F. Scand. nos. 292a and 292b.

The synonymy of the fungus is as follows: *Systremma Ulmi* (Schleich.) Thiess. and Syd., Die Dothidiales, Ann. Myc. **13**:334. 1915; *Sphaeria Ulmi* Schleich., Crypt. Exsic. no. 73, sec. de Candolle Fl. Franc. **2**:288. 1805; *Sphaeria xylomoides* DC., Fl. Franc. **2**:288. 1805; *Sphaeria Ulmi* Duv., Hoppe's Bot. Taschenb., 105. 1809; *Xyloma sticticum* Mart., Crypt. Flor Erlang., 309. 1817; *Sphaeria ulmaria* Sow., Eng. Fung., *pl. 374. fig. 3; Polystigma Ulmi* Link, Rab. Handb. **1**:167; *Dothidea Ulmi* Fr., Syst. **2**:555. 1823; *Phyllachora Ulmi* Fuck., Symb. 218; Sacc. Syll. Fung. **2**:594. 1883; *Euryachora Ulmi* Schroeter, Crypt. Fl. Schles. 3^2:473.

The conidial stage of this fungus is *Piggotia astroidea* B. and Br.

Other leaf spots of elm

IN AMERICA

MYCOSPHAERELLA ULMI Kleb. (**28**).—This is the ascigerous stage of *Phleospora Ulmi* (Fr.) Wallr., which has been reported both in America and Europe as the cause of a leaf spot on *Ulmus campestris, U. glabra*, and *U. americana*. In the conidial stage it is said sometimes to do considerable damage to nursery stock and young trees. STEWART (**36**) states that it has been observed several times to cause extensive defoliation of young elms in New York. Numerous, small, reddish-brown spots appear on the upper side of the leaves, which in consequence gradually turn yellow, the margin becomes brown and rolls up, and they fall early in the season. The spores ooze out in minute cirrhi which dry on the lower side of the leaf surface and form small whitish patches. SACCARDO (**31**) states that on account of the absence of pycnidia it leans toward *Septogloeum*, and it is sometimes known by that

name. CLINTON (9) and BRIOSI and CAVARA (5) also maintain that it belongs to that genus and call it *Septogloeum Ulmi* (Fr.) Bri. and Cav. CLINTON also suggests that *Cylindrosporium ulmicolum* Ell. and Ev. is possibly not distinct from this species. I have not seen the ELLIS and EVERHART specimen, and admittedly the two descriptions are very similar, especially when one takes into consideration the very great differences in spore measurements recorded by various collectors of *Phleospora Ulmi*. STEWART records as follows: "As we have found them, they (the spores) are 3- or 4-septate, usually quite strongly curved, and measure 34–38×5.5–6.5 μ. In no. 157 of *Seymour* and *Earle's* Economic Fungi, on *Ulmus fulva*, the spores are 3-septate, straight, and measure 33.5×6.3 μ. In no. 648 of *Krieger's* Fungi Saxonici, on *Ulmus campestris*, they are 3- or 4-septate, strongly curved, and measure 49.5×4.7 μ." Under the name of *Septoria Ulmi* Fr., this fungus was regarded by FUCKEL as the spermagonial stage of *Phyllachora Ulmi*, a synonym of *Systremma Ulmi*, but it was shown by KLEBAHN (23) that it had no connection with that fungus, but was the conidial stage of *Mycosphaerella Ulmi*, which develops on the dead leaves in the spring.

CYLINDROSPORIUM ULMICOLUM Ell. and Ev.—Spots becoming flavous; acervuli minute, hypophyllous; conidia cylindraceous, 45–65×4 μ, hyaline, multinucleate, coming out in minute white caespitules. Reported on leaves of *Ulmus alata* in Mississippi. In spite of the differences in spore measurements, the possibility has been suggested that this is not different from *Phleospora Ulmi*.

SEPTOGLOEUM PROFUSUM (Ell. and Ev.) Sacc.—Spots epiphyllous, flavous; acervuli scattered, hypophyllous, large; conidia coming out in white cirrhi, cylindrical, oblong, granular, 3-septate, 25–30×6–7 μ. Reported on living leaves of *Ulmus americana* and *U. alata*, although it was first described on *Corylus americana*.

CERATOPHORUM ULMICOLUM Ell. and Hark.—Causes small, suborbicular, dirty-brown, amphigenous spots with a white center, 0.5–1 cm. in diameter, on living leaves of *Ulmus fulva*. Noted from several places in the United States.

PHYLLOSTICTA ULMICOLA Sacc.—Reported as being present in Wisconsin by DAVIS (13) who states as follows:

Under this name I am recording the occurrence of a fungus having the following characteristics: Spots indefinite, immarginate, orbicular, light-brown, becoming cinereous above and lacerate, finally falling away in fragments, 3–7 mm. in diameter, sometimes confluent; pycnidia epiphyllous, scattered, black, globose to depressed, 60–80 μ; sporules globose to elliptical, olivaceous-hyaline, continuous, 3–6×2–3 μ. On *Ulmus americana*, Tisch Mills, August 3, 1917. *Ulmus racemosa*, August 5, 1917. This is probably a member of a group of forms of which various names have been applied in Europe and America.

It has also been reported from a number of other states, among them Michigan, where it is said to occur on *Ulmus fulva*.

PHYLLOSTICTA CONFERTISSIMA Ell. and Ev.—Spots red-black, amphigenous; pycnidia 75 μ in diameter; spores allantoid, hyaline, 3–4×1 μ. On leaves of *Ulmus fulva* in Kansas.

PHOMA CINCTA B. and C.—Spots irregular, depressed, with a white border; spores oblong, narrow, 6–8 μ long. Reported on leaves of *Ulmus americana* in South Carolina.

EXCIPULA ULMICOLA Schw.—Causes widely expanded indeterminate spots on the upper side of the leaf, becoming somewhat spotted with gray on both sides, with a broad, fuscous margin; pycnidia copious, immersed, excipuloid, punctiform, black, depressed in center and becoming gray. Reported as somewhat rare on cast-off leaves of *Ulmus fulva* about Bethlehem, Pennsylvania.

CORYNEUM TUMORICOLUM Peck.—Forming scattered, suborbicular, pale spots, bounded by a red-brown border on living leaves of *Ulmus americana* in the Adirondack Mountains.

SPHAERIA APERTIUSCULA Schw.—Scattered, fuscous-black, minute, arising from the swollen parenchyma; at first innate, at length opening by a very wide mouth, but evacuate within; resembles a small *Peziza*. Recorded as occurring on the lower side of leaves of *Ulmus fulva* in New York.

RHYTISMA ULMI Fr.—Minute, difformous, gyrose with an elevated margin, at length dehiscing labiately. Reported on leaves of *Ulmus* in North America.

MELASMIA ULMICOLA B. and C.—Spots reddish, indefinite; pycnidia punctiform; spores minute, oblong-botuliform. COOK (10) speaks of it as the *Melasmia* stage of *Rhytisma Ulmi*, and reports it as very common in New Jersey.

List of species occurring in Europe only

Acremoniella pallida Cooke and Mass., *Actinonema Ulmi* Alleschr., *Ascochyta ulmella* Sacc., *Asteroma angulatum* Desm., *A. Fuckelii* Sacc., *Cladosporium hypophyllum* Fuck., *Exoascus campester* Sacc., *Gloeosporium inconspicuum* Cav., *G. inconspicuum* Cav. var. *campestris* Dor., *Laestadia comedens* (Pass.) Sacc., *Pestalozzia maculicola* Rostr., *Phyllosticta bellunensis* Mart., *P. lacerans* Pass., *P. ulmaria* Pass., *P. Ulmi* West., *Sphaerella Oedema* (Fr.) Fuck., *S. insularis* Wallr., *Sphaeria ulmifolia* Pass., *Sporodesmium Ulmi* Fuck., *Stagonospora ulmifolia* (Pass.) Sacc., *Stigmella Castagneana* (Mont.) Sacc., and *Taphrina Ulmi* Johans.

Fossil leaf spots of elm

In Meschinelli's *Fungorum Fossilium Iconographia* seven species are given occurring on leaves of fossil elms. Plates and figures are included for six of these, but they are very unsatisfactory in most cases, and in some instances one cannot be at all sure that the spot is even of fungal origin. The species are as follows: *Sphaerites perforans* Goepp., *S. glomeratus* (Engelh.) Mesch., *S. rhytismoides* (Ettingsh.) Mesch., *Rhytismites ulmicola* (Ettingsh.) Mesch., *R. Ulmi* (Ludw.) Mesch., *Depazites Ulmi* (Ettingsh.) Mesch., and *Xylomites* sp. (Boulay) Mesch.

Summary

1. *Gnomonia ulmea* (Schw.) Thüm., the cause of the most common elm leaf spot in America, has been reported as occurring on five of the six native species of elm in this country and is of wide distribution, being found throughout the entire range of its hosts. Its normal host, on which it is most commonly found, is *Ulmus americana*. The fungus is not ordinarily of much economic importance, but may cause considerable injury to seedlings and young trees in nurseries by producing premature defoliation.

2. Unlike most of the Ascomycetes, the perithecial stage of the fungus begins its development in the living leaf early in the spring. The young perithecium develops in the palisade tissue beneath a subcuticular black stroma.

3. An ascogonium is found in the young perithecium, but there is no trichogyne.

4. An interascicular pseudoparenchyma is found present in the perithecium almost until the period of maturity.

5. In the process of ascospore expulsion an entire ascus enters the lower part of the ostiolar canal, and the eight spores are apparently discharged simultaneously.

6. The ascospores could not be made to germinate either in tap or distilled water, in nutrient solutions, on solid media, or on the living leaves of the English or Scotch elm. They germinated readily on the leaves of the American elm, however, thus indicating that they require a special stimulus of some sort which is present in the leaves of some species of *Ulmus*, but absent in others.

7. The fungus matures most rapidly during the winter on leaves which are neither too exposed nor in too damp a situation. When immersed in water or in intimate contact with the soil, the fungus dies, and only the empty husks of the perithecia remain.

8. A conidial stage was found constantly associated with this ascigerous form. It is described as a new species, *Gloeosporium ulmeum*.

9. The connection between the two forms was conclusively proven by inoculations. The ascospores of *Gnomonia ulmea* gave rise to spots on the leaves of *Ulmus americana* which were entirely typical of *Gnomonia*, and which bore the acervuli of *Gloeosporium ulmeum*. The spores of this form also readily infected the leaves of the American elm, and appeared even more virulent than were the ascospores, indicating that this form is probably the agent by which extensive dissemination of the fungus is assured in spring and early summer.

10. A new leaf spot of the American elm, caused by *Gloeosporium ulmicolum*, another new species, is described. This species differs from the one previously described in the characters of the spot and in the larger size of the spores.

11. *Systremma Ulmi* (Schleich.) Thiess. and Syd. causes a leaf spot of the European elms in Europe. *Gnomonia ulmea* has been very much confused with this fungus, and as a consequence has gotten into the literature as occurring in this country. The probability is, however, that it does not occur in America at all.

It is a member of the Dothidiales, while *Cnomonia ulmea* belongs to the Sphaeriales.

12. Other species of fungi producing leaf spots on the elm are listed with a brief comment on each of the American forms.

13. Seven species of fungi are listed on the leaves of fossil elms.

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EXPLANATION OF PLATES VIII–X

PLATE VIII

FIG. 1.—Two perithecia of *Gnomonia ulmea* in almost mature condition, showing interascicular pseudoparenchyma, and also elongated beaks and periphyses-lined ostiolar canal.

FIG. 2.—Early stage in development of perithecium of *Gnomonia ulmea*, showing position in palisade layer; subcuticular stroma above has given rise to acervulus of imperfect form of fungus, *Gloeosporium ulmeum*.

FIG. 3.—Elm leaf, showing one type of *Gnomonia* spot; note absence of border of dead or browned tissue and that stromata tend to coalesce.

FIG. 4.—Elm leaf, showing another type of spot; black stromata surrounded by border of light brown dead tissue.

FIG. 5.—Same as fig. 4 except that epidermis covering stromata has begun to wear away, giving spot a lighter, somewhat ashen, appearance.

PLATE IX

FIG. 6.—Leaf of English elm, showing leaf spot caused by *Systremma Ulmi;* note that each spot is but a single stroma, much more definite in outline than that caused by coalesced stromata of *Gnomonia ulmea*, and that they are raised much more above surface of leaf; note also wrinkled or papillate appearance of stroma.

FIG. 7.—Schweinitzian type specimen of *Gnomonia ulmea.*

FIG. 8.—Perithecium of *Gnomonia ulmea* at earliest stage in development of beak and ostiole; dark portion of perithecium represents young asci just beginning development; note psuedoparenchymatous contents of perithecium.

FIG. 9.—Elm leaf, showing spots caused by *Gloeosporium ulmicolum*, sp. nov.; note manner in which spots follow the veins; compare with figs. 3, 4, 5, 7, and 12 for differences from spot caused by *Gnomonia ulmea.*

FIG. 10.—Section through stroma of *Systremma Ulmi*, subepidermal in origin; note absence of perithecial walls, and that asci are borne in locules in stroma which open on upper side of leaf.

FIG. 11.—Single spot, fig. 12*a*, enlarged 10 diameters, showing isolated character of stromata of *Gnomonia ulmea.*

FIG. 12.—Elm leaf, showing stromata of *Gnomonia ulmea* as they sometimes appear, widely separated in spot and somewhat concentrically arranged.

FIG. 13.—Very young stage in development of perithecium of *Gnomonia ulmea*, showing pyriform shape at this stage, and connection with stroma.

PLATE X

FIG. 14.—Acervulus of conidial stage, *Gloeosporium ulmeum*, sp. nov., formed above young perithecium of ascigerous stage, *Gnomonia ulmea.*

FIG. 15.—Spores of *Gloeosporium ulmeum.*

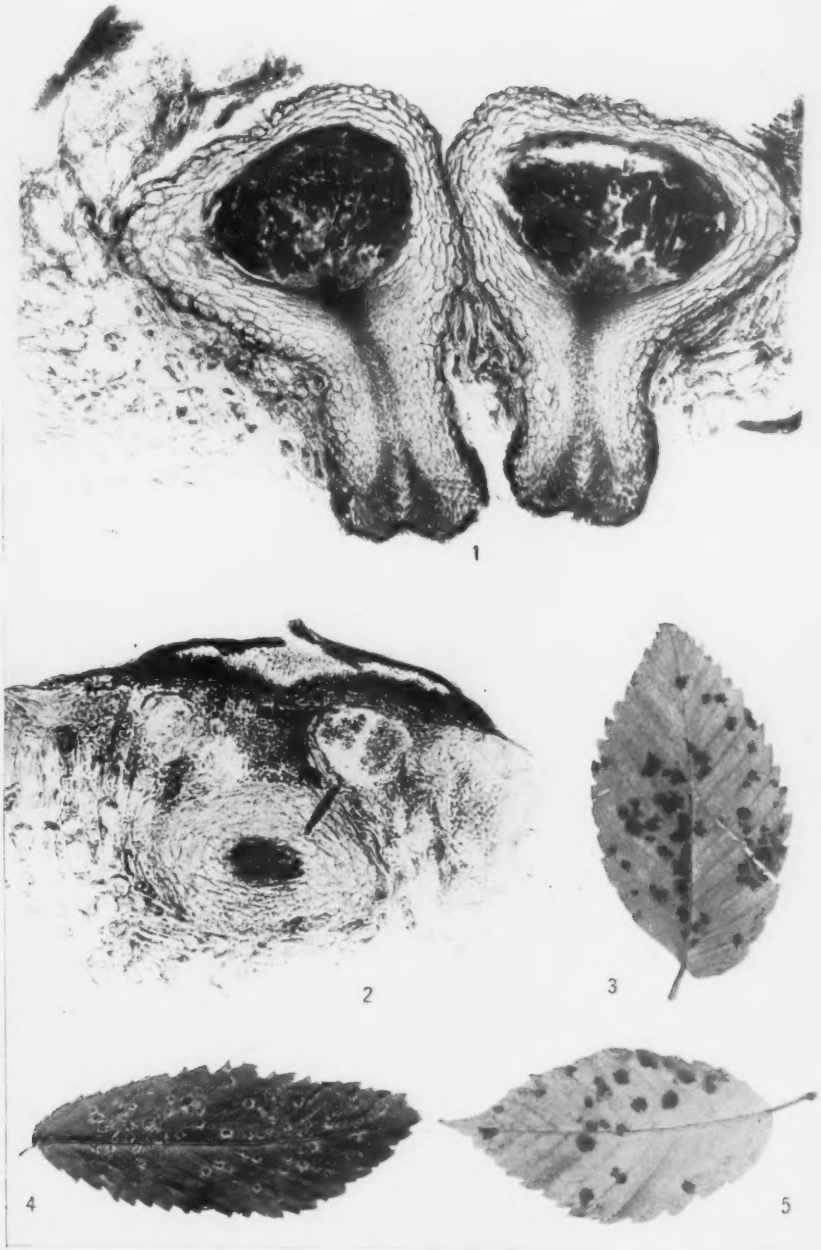
FIG. 16.—Very young stage in development of *Gnomonia ulmea: a*, sheathing hypha; *b*, ascogonium; *c*, "suspensor" or "infection thread"; *d*, vegetative hyphae which break through stroma to outer surface.

FIG. 17.—Spores of *Gloeosporium ulmicolum.*

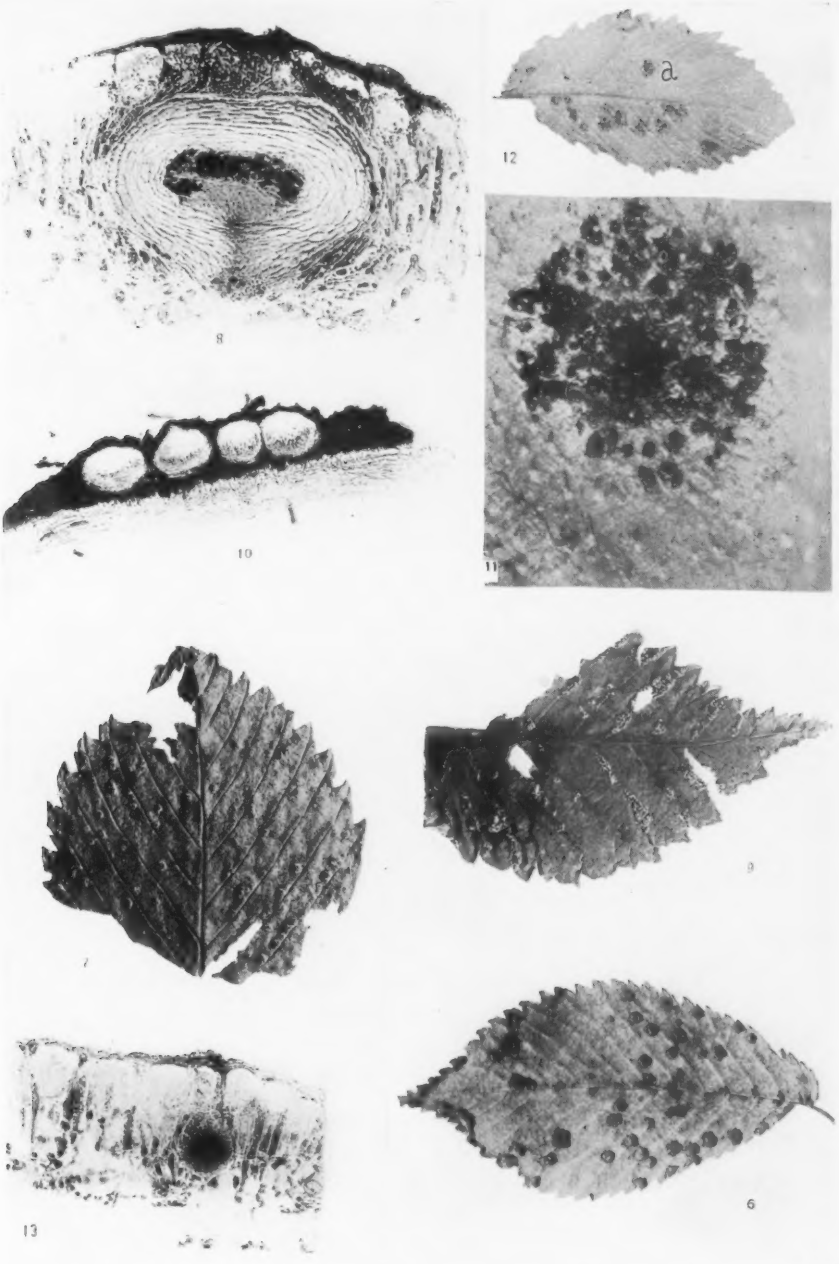
FIG. 18.—Single acervulus of *Gloeosporium* stage of *Gnomonia ulmea*, showing manner of cracking to allow dispersal of spores; hyphae about acervulus are those of basal stroma as viewed from above.

FIG. 19.—Ascus and ascospores of *Gnomonia ulmea.*

FIG. 20.—Germinating spores of *Gnomonia ulmea.*



MILES on LEAF SPOTS



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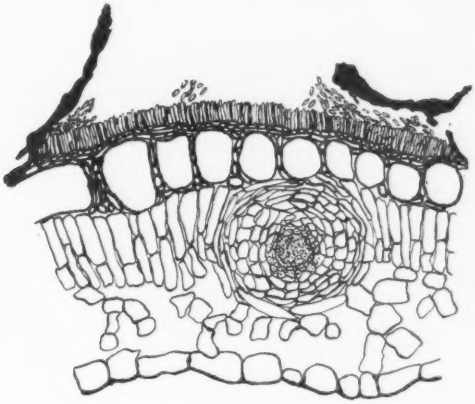

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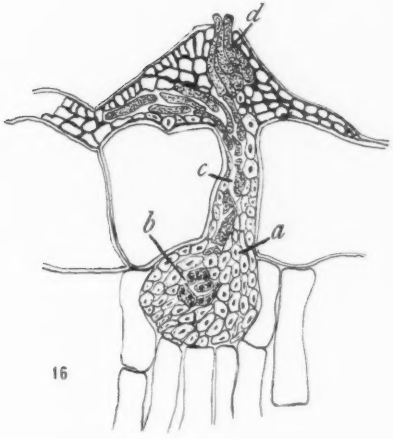

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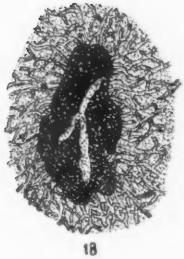

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MILES on LEAF SPOTS

INFLUENCE OF ENVIRONMENT ON SEXUAL EXPRESSION IN HEMP[1]

JOHN H. SCHAFFNER

(WITH PLATE XI AND ONE FIGURE)

The study of hemp, *Cannabis sativa* L., was originally undertaken by the writer to determine what influence the environment might have on the sex ratio between staminate and carpellate plants. During the progress of the investigation, other problems in relation to sex presented themselves which were of more immediate importance than the mere determination of the factors which might be the cause of variation in the expected number of staminate or carpellate individuals. The first plantings were made in the fall of 1913, but little was accomplished at that time because the department of botany was preparing to move into a new building, and, as is commonly the case in such ventures, several years were consumed in bringing the new plant into proper working order. The investigation was resumed in the fall of 1916, from which time on plantings have been made each year out of doors in the spring and each winter in the greenhouse, excepting the winter of 1917–1918, which was spent in Florida.

As stated, it soon became evident that far more fundamental problems were presented for solution than the mere changing of sex ratios. Intermediate plants appeared, bearing both stamens and carpels. There was also an endless profusion of abnormal flowers involving all sorts of sexual expressions; and, most remarkable of all, complete reversal of sexual expression under the influence of an abnormal environment presented itself as the most interesting phenomenon to be studied. The last three years, therefore, have mainly been devoted to a study of abnormal flowers and sex reversal.

Examination of the plants in the beds was greatly facilitated by the use of a Bausch and Lomb binocular magnifier. The

[1] Papers from the Department of Botany, the Ohio State University, no. 120.

detailed study of flowers and other parts was carried on mainly with the aid of a binocular dissecting microscope.

Previous reference to the abnormal behavior of the hemp under the imposed abnormal conditions was made by the writer (3) as follows: "Not only did typical staminate plants sometimes produce bisporangiate flowers with more or less normal gynoecia, but some carpellate plants even produced stamens. This in spite of the fact that the plants were differentiated in their vegetative parts as typically carpellate." A preliminary notice (5) of the complete reversal of sex was published in 1919. In 1916 PRICHARD (2) published the results of experiments on hemp, in which changes in sexual expression were shown to take place as the result of various treatments, such as removal of flowers, etc.

Record of seed and plantings

The original seeds were bought from a seed house in Columbus, Ohio, their origin being unknown.

Plot 1, planted January 1917, in botanical greenhouse. Numerous sex intergrades and sex reversals were observed. Intermediate plants and abnormal flowers studied.

Plot 2, planted in the garden May 1918, with part of the original seeds. The plants were apparently all pure carpellate and pure staminate. No intermediates of any kind were found.

Plot 3, planted in the greenhouse on December 23, 1918. Seeds from individual plant of plot no. 2. Flowers began to open February 1, 1919. There were 73 carpellate and 77 staminate plants. Many were intermediate in sexual expression, or later reversed their sexual condition. These plants were mainly studied for abnormalities in sexual expression in the flowers.

Plot 4, planted in the greenhouse January 22, 1919. Plants in bloom on March 17. Seeds from an individual of plot 2.

Plot 5, planted in the greenhouse February 1, 1919. Seeds from an individual of plot 2. Seeds came up February 6 and 7. Plants began to bloom March 5.

Plot 6, planted in the garden early in May 1919. Seeds from an individual of plot 2. In this plot there were 124 pure carpellate and 122 pure staminate plants. There were no intermediates and no sex reversals of any kind.

Plot 7, planted in the garden June 24, 1919. Seeds from a plant of plot 2. In bloom August 18. There were 86 pure carpellate and 83 pure staminate plants. No intermediates or reversals of any kind appeared.

Plot 8, planted in the greenhouse November 26, 1919. Seeds from a red colored individual of plot 7. First flowers opened January 6, 1920. Plants dying and the last pulled up May 12, 1920.

Plot 9, planted in the greenhouse November 26, 1919, with seeds from a normal green leaved individual from plot 7. First flowers opened January 6, 1920. All the plants had been pulled up or were dying May 12, 1920.

Plot 10, planted in the greenhouse on the north side December 4, 1919, with seeds from an individual of plot 7. First flowers in bloom January 13, 1920. All the plants had reversed their sex or were dying by May 4, 1920.

Plot 11, planted in the greenhouse on the north side December 19, 1919. Seeds from an individual of plot 7. The plants had two pairs of leaves when the flowers began to open January 30, 1920. All of the plants had reversed their sex or were dying May 1, 1920.

Plot 12, planted in the greenhouse on the north side on December 19, 1919. Seeds from the red leaved individual used for plot 8. Flowers began to open on February 1, 1920, when most of the individuals had but two pairs of leaves. All of the plants had reversed their sex or were dying May 4, 1920.

Plot 13, planted in the greenhouse on December 19, 1919. Seeds from the same red leaved individual as used for plots 8 and 12. Flowers began to open February 6, 1920. All plants had shown sex reversal or were dying and pulled up by May 12, 1920.

Plot 14, planted December 19, 1919, in the greenhouse with seeds from an individual of plot 7. Flowers were opening on February 6, 1920. All plants had reversed their sex or were dying and pulled up by May 12, 1920.

Plot 15, consisting of special plantings from seeds obtained from individuals raised in the greenhouse in the winter of 1918–1919: (1) Seeds from a plant which produced staminate flowers before it died; two plants were obtained, one staminate and one

carpellate; both were intermediate in sexual expression and of the same character as intermediate plants obtained from seeds from pure parents; (2) seeds from a carpellate plant which developed three staminate flowers before it died; three plants were obtained, which were carpellate but produced stamens before they died; two individuals became decidedly staminate and one slightly so; (3) seeds from an apparently pure carpellate plant but pollinated with pollen from an intermediate staminate plant; two carpellate plants were secured which later produced stamens.

Cultural conditions

The various plantings in the garden were perfectly normal, and not a single individual gave any indication of an intermediate or monoecious condition, and there was no sex reversal. The plants raised in the greenhouse during the winter were growing in a very abnormal environment. The aim was to change the environmental factors controlling growth and nutrition as much as possible without interfering entirely with reproduction. Accordingly a rich soil was used, with abundance of water and the ordinary temperatures used in greenhouses during the winter months. The light conditions were very low, the soil in the benches was shallow, about 3 in. deep, and the main source of heat was immediately beneath the benches. Under these conditions the hemp matured very early, and in those plants which had the poorest illumination the inflorescence usually appeared when but two pairs of leaves were present. The plants were never more than a few inches high, and the first staminate flowers usually opened in 32 or 33 days from the time of planting.

No attempt was made to discover which abnormal condition or set of conditions was mainly responsible for the changed morphology and sexuality, but apparently the reduction in the quantity and intensity of light, with its effect on the nutritive process, is the chief factor involved. Good illumination with low temperature would probably give much the same results. The influence of the abnormal conditions on sexual expression, as will appear later, is very great. Commonly more than 75 per cent of the individuals showed mixed sexual expression or a reversal of the sex before the

end of life. The staminate plants usually began to die soon after the first inflorescence had come to bloom, while the carpellate plants usually lived for several months, after the first seeds had ripened, and continued to bloom from new lateral branches. Occasionally a carpellate plant was entirely rejuvenated and put out a second system of shoots which had all the signs and characteristics of the original sprout coming from the seed. A few staminate plants transplanted and carefully nurtured also showed some rejuvenation and continued to produce branches below for some time, but they mostly became senile and died after the blooming of the first inflorescence was completed.

FIG. 1.—*Cannabis sativa:* staminate (*a*) and carpellate plant (*b*) of same age, grown in greenhouse in winter, showing decided sexual dimorphism; each plant showed reversal of sex and produced sporophylls of opposite nature; plants transferred from plot in greenhouse to pots just before being photographed.

Sexual dimorphism

Hemp as grown under normal conditions is distinctly dimorphic, both as to flowers and vegetative characters. The vegetative dimorphism, however, is much greater in plants grown under the abnormal greenhouse environment (text fig. 1, *a* and *b*). The plants experimented with, of course, had their sexual state already established in the embryo of the seed, and whatever changes were induced had their origin during the vegetative growth, between the period of sprouting and the origin of the incepts of the opposite types of flowers. This must be true for all plants, except perhaps for the few intermediate individuals in which the confused condition of sexual expression might have been due to a definite genetic constitution which would allow of a mixed sexual

expression under any ordinary environmental conditions. The only other available hypothesis, according to the writer's views, would be to assume that sex is not determined in the seed, but only after vegetative growth has begun.

The ratio between carpellate and staminate plants is 1:1, with considerable fluctuation in either direction for any given planting. The vegetative dimorphism is the same for individuals which show no tendency to change their sexual expression and those which do so sooner or later. The main sexual differences are as follows.

Carpellate plant.—A broad flat crown of leaves; vigorous appearance but not so tall as the staminate plant; robust stem; large root system; large leaf blades with more numerous leaflets, usually five or more; terminal inflorescence usually leafy; petioles longer and more robust; carpellate flowers with the perianth a closed sacklike sheath with no vestigial stamens; weight at beginning of the flowering period nearly twice as much as that of the staminate plant of the same age; a longer period of life and growth.

Staminate plant.—A slender, spindling habit and taller than the carpellate plant through the very rapid elongation of the internodes just before anthesis; root system smaller than in the carpellate plant; smaller leaf blades with fewer leaflets; shorter and more slender petioles; terminal inflorescence with few or no leaves; staminate flowers with 3–6 separate sepals (usually 4 or 5) with no vestige of a gynoecium; weight about half that of the carpellate plant at time of anthesis; a much shorter life than the carpellate plant.

The weights of a dozen individuals of the same age, from the same plot, were determined as follows. Staminate and carpellate plants were cut off at the cotyledon node and immediately placed in glass jars with ground glass stoppers. They were thus weighed without loss of water. After weighing, the stoppers were removed and the jars with the specimens kept in the oven at 50°C. After three days they were placed in an oven at 110°C. and heated for two hours. The stoppers were then replaced, and after cooling the final weights were made of the dried plants. Table I gives the individual weights, the totals, and the averages. It will be seen that the carpellate plants average nearly twice the weight

of the staminate plants. Probably if the root systems had also been weighed the ratio would have been very nearly 2:1. Apparently there is very little if any difference in the ratio between the dry matter and water of the carpellate plants and that of the staminate plants. On account of the decided vegetative dimorphism of the winter plants, a number of interesting differential physiological studies might easily be carried on with the hemp.

TABLE I

WEIGHTS OF 12 PLANTS AT BEGINNING OF ANTHESIS

PLANT NO.	CARPELLATE			PLANT NO.	STAMINATE		
	Green weight	Dry weight	Water		Green weight	Dry weight	Water
1...	3.35 gm.	0.58 gm.	2.77 gm.	2...	1.91 gm.	0.38 gm.	1.53 gm.
3...	3.01	0.62	2.39	4...	2.25	0.34	1.91
5...	2.70	0.52	2.18	6...	1.47	0.31	1.16
7...	2.42	0.44	1.98	8...	2.17	0.41	1.76
9...	2.95	0.53	2.42	10...	0.87	0.17	0.70
11...	2.58	0.45	2.13	12...	1.03	0.20	0.82
Total	17.01	3.14	13.87	Total	9.70	1.81	7.89
Average.	2.835	.523	2.311	Average	1.616	.301	1.315

Abnormal, irregular, and bisporangiate flowers

Plots 1 and 3 were mainly studied for irregularities in the flowers. These were so remarkable that chief attention was diverted to their morphology in relation to sexual expression, while the remaining greenhouse plantings were studied for sex ratios and sex reversals. In all the winter plantings there was a great assortment of sexual expression in the flowers. One could find almost any conceivable combination of perfect and imperfect sporophylls. Figs. 1–12 were selected, not as an exhaustive set of examples, but simply to indicate the general character of the confusion displayed by the spore bearing organs. They show that any attempt to bring these sexual expressions within the bounds of Mendelian heredity would be out of the question. Fig. 1 is a typical staminate flower from a staminate plant, and fig. 2 is a normal carpellate flower, with the sheath cut open,

from a carpellate plant. The staminate flower has four distinct sepals and the normal gynoecium has two stigmas. In some cases nearly typical carpellate flowers appear on staminate plants (fig. 3), and carpellate plants often bear normal staminate flowers toward the end of their life. A common abnormality is the development of a typical stigma or one of varying degrees of perfection at the outer end of an anther (figs. 4, 7, 9*a*, also 6, 8, 11). Occasionally a stamen grows directly out of the side of an ovulary (fig. 5), or the ovulary may have more or less perfectly developed microsporangia on one side. Fig. 10 represents such a structure from the tip of the inflorescence of a carpellate plant. This flower has the characteristic staminate perianth, although in other respects it is more carpellate in nature. Figs. 6 and 7 represent two types of abnormal flowers, both from a carpellate plant. Fig. 6 has one good and nearly normal stamen. Fig. 8 is a stamen-carpel complex from the center of a staminate flower with four normal stamens, taken from a staminate plant. Apparently an attempt was made to develop a normal bicarpellary gynoecium. The one side has an imperfect ovulary with a normal stigma, while the other has a distorted anther with two microsporangia ending in an imperfect stigma. Figs. 9 and 9*a* represent a flower from a staminate plant with an imperfectly developed gynoecium in the center. The separated stamen (fig. 9*a*) has a well developed stigma, and one other stamen has a rudimentary structure at the tip which shows a slight development in the direction of a stigma. Fig. 11 represents a staminate flower from a carpellate plant with three stamens on a central stalk, the normal position for the gynoecium, two of the stamens having rudimentary stigmas. Fig. 12 is an imperfectly bisporangiate flower from a staminate plant. As intimated, a great number of such variations and abnormalities of every conceivable diversity appear on both staminate and carpellate plants. They are readily intelligible on the theory that they are caused by varying and reversible sexual states. Any attempt to bring such phenomena within the limits of discrete Mendelian units, segregated and combined normally or abnormally during the reduction and fertilization stages, would appear extremely absurd to the writer.

Diversity of flower types on individual plants

Plant no. 1, a carpellate plant which had besides the normal carpellate flowers: two flowers each with 3 stigmas united below; one flower with 3 small but perfect stamens and a gynoecium with 2 stigmas; one flower with 3 sepals and a gynoecium with 1 stigma; one flower with 4 sepals, 1 stamen, and a gynoecium with 3 stigmas.

Plant no. 2, a staminate plant which had besides the numerous normal staminate flowers: one carpellate flower with a normal gynoecium with 2 stigmas but with 4 small sepals; one flower with 4 sepals and a central structure developed as a stamen on one side ending in a stigma and an ovulary on the other also ending in a stigma; one staminate flower with 4 sepals, 2 normal stamens, 1 rudimentary stamen, and 1 stamen with a stigma projecting from its side; one staminate flower with 4 sepals, 1 normal stamen, and 1 structure with 2 microsporangia and a rudimentary ovulary with 2 stigmas; one flower with 5 sepals and a central structure, part stamen with 4 microsporangia and a rudimentary ovulary with 2 stigmas; one staminate flower with 4 sepals, 4 normal stamens in a cycle, 1 centrally placed normal stamen, and beside this a rudimentary ovulary with a normal stigma; one staminate flower with 6 sepals, 5 normal stamens in a cycle, and a central stamen which was thick and short; one staminate flower with 5 sepals and with 5 stamens in a cycle one of which ended in a stigma; one flower with 4 sepals, 4 stamens, and 1 apparently normally placed central ovulary with a stigma and beside this a rudimentary ovulary also ending in a stigma; one flower with 5 sepals, 5 stamens, and a central rudimentary gynoecium with stigma.

Plant no. 3, a carpellate plant which had besides normal carpellate flowers: one flower with 4 sepals, 2 normal stamens, and a central rudimentary ovulary with 2 stigmas; one flower with 4 sepals, 3 normal stamens, and a carpellate structure with 5 stigmas; one flower with 4 sepals and a bladdery ovulary with 4 stigmas.

Plant no. 4, a carpellate plant which had besides numerous normal carpellate flowers: one carpellate flower with a microsporangium in the side of the ovulary; one staminate flower with

5 sepals and 4 stamens, one of the stamens with 2 microsporangia and stigma; one flower with a gynoecium with 2 stigmas, and a normal stamen connected with the base of the ovulary; one flower with 3 sepals, 2 normal stamens, and 2 stamens grown together by their filaments, the one with 4 microsporangia and a rudimentary ovulary in its side, the other with 2 microsporangia and an ovulary with a normal stigma in its side; one staminate flower with 2 sepals and 3 normal stamens; one staminate flower with 4 sepals and 2 normal stamens.

Plant no. 5, a staminate plant having besides the usual types of staminate flowers: one flower with 3 sepals, 3 stamens, and in the center 1 normal carpel with a stigma and 1 rudimentary carpel with a stigma; one flower with 6 sepals, 4 normal stamens, 1 rudimentary stamen, and a central gynoecium with 3 stigmas; one flower with 5 sepals, 3 normal stamens, and a central structure staminate on one side with 4 microsporangia, and carpellate on the other side with a typical stigma; one flower with 5 sepals and 5 stamens, one of the stamens with a stigma; one flower with 5 sepals, 2 normal stamens, a rudimentary structure of indefinite nature, and a gynoecium with 1 normal stigma and 1 rudimentary stigma.

Such is the usual character of the plants with reversed and confused sexuality. They can be obtained in great numbers in the winter and are very convenient for study. There is also much diversity in the time and degree of reversal of the sexual state in the long-lived carpellate individuals. Two individual records follow:

Plant no. 1 was a decidedly carpellate plant which produced eight seeds and was strong and vigorous. It sprouted at the lower nodes of the inflorescence and produced abundant carpellate flowers on these branches also, while the top of the main stem was dying off. This plant was at first taken to be a pure carpellate individual, but later two flowers developed on a branch, each with a fully developed stamen.

Plant no. 2 was a carpellate plant which produced seed and later developed a lateral branch with typical carpellate flowers, and at the same time continued to grow at the tip of the main axis on

which a staminate flower was produced. One cannot tell, therefore, whether a plant will continue "pure" or whether it will reverse its sexual state until it actually begins to die.

Sex intergrades and sex reversals

Plots 2, 6, and 7 were planted out of doors under normal conditions. Not a single intermediate plant was developed, and not a sign of sexual confusion in the floral characters was found. Plots 6 and 7 were studied with great care. No record was kept of the ratio between staminate and carpellate plants of plot 2. Plot 6 had 124 carpellate and 122 staminate plants, all absolutely pure in sexual expression. Plot 7 had 86 carpellate and 83 staminate plants, all pure as to sexual expression. Plots 4, 5, 8, 9, 10, 11, 12, 13, and 14 were studied for sex ratios and ratios of pure plants to those of mixed sexual expression. The numbers of carpellate to staminate plants in the greenhouse experiments, of which definite records were kept, are shown in table II.

TABLE II

Plot no.	Carpellate plants	Staminate plants
3	73	77
4	114	132
5	53	39
8	44	41
9	43	34
10	23	30
11	18	13
12	36	17
13	43	31
14	47	23
Total	494	437

The percentages of plants with mixed sexual expression to those of pure sexual expression are given in table III. The plants were removed as soon as they showed a definite reversal to the opposite sexual state, or if they had not reversed they were pulled up when they began to die. In the nine plots which were studied for purity, reversal, or mixed sexual characters, therefore, the following proportions were found. Out of a total of 421 carpellate plants 167 were pure and 254 were of mixed sexual expression, or 39+

per cent pure and 60+ per cent mixed. Of the 360 staminate plants 144 were pure in sexual expression and 216 mixed, or 40 per cent pure and 60 per cent mixed. It will be noted that a much higher percentage of intermediates was obtained in the plantings of the winter of 1919–1920 than in the winter of 1918–1919. This is apparently due to the fact that the plants in 1919–1920 received the minimum amount of light, since the plantings were made in November and December, instead of in January and February. Plots 11 and 12 show the greatest degree of reversal of sex, and these plots were planted on December 19 in the north side room of the greenhouse which receives the minimum amount of light and was also kept at a lower temperature.

TABLE III

Plot no.	Carpellate plants		Staminate plants	
	Pure	Mixed	Pure	Mixed
4	60	54	75	57
5	23	30	19	20
8	25	19	12	29
9	19	24	5	29
10	7	16	13	17
11	2	16	2	11
12	4	32	4	13
13	17	26	9	22
14	10	37	5	18
Total	167	254	144	216

The ratios of plot 11 are as follows: carpellate individuals, 11+ per cent pure carpellate and 88+ per cent intermediates; staminate individuals, 15+ per cent pure staminate and 84+ per cent intermediates. Taking the two plots together the ratio is 11+ per cent pure carpellate to 88+ per cent intermediate carpellate, and 20 per cent pure staminate to 80 per cent intermediate staminate. It is probable that if these plants had been more carefully spaced and cared for, every individual, both staminate and carpellate, would have developed both sexual states sooner or later.

It will be noted that the plants of plots 8–14 had two generations of known sporophyte ancestors which had shown no confusion of sex. Plots 3, 4, 5, 6, and 7 had pure sporophyte parents, but plots

3, 4, and 5 produced large numbers of intermediates and reversals, while plots 6 and 7 produced only pure carpellate and pure staminate plants. It is evident, therefore, that the large numbers of intermediates and reversals of plots 3, 4, and 5 were due entirely to the conditions of environment and not to a difference in genetical constitution as compared with the plants of plots 6 and 7. The abnormal environment caused a reversal in the staminate seedling from the male to the female state, and this resulted in the expression of carpellate structures in varying degrees of extent and intensity. The same environmental conditions caused a reversal in the carpellate plants from a female to a male condition, either in the early seedling stage or at any later time until the approach of old age and death. This reversal is also of varying degrees of extent and intensity as in the staminate plant. In extreme cases the carpellate plants produced normal stamens with fully developed pollen, which is shed in the usual manner. In other cases, although stamens were developed, the pollen was imperfect and the anthers dried off without dehiscing. In the reversal of the staminate plant there were also occasional normal carpellate flowers produced with their entire morphology typically carpellate, but usually the structures were abnormal.

Enough progress has now been made in the direction of sex control in the hemp to take a quantity of seeds and produce at will either a stand consisting of individuals with pure male or female expression, pure staminate or carpellate plants, or a stand of individuals in which 50–90 per cent are of mixed sexual expression, although the sex was apparently already definitely determined as male or female in the sporophyte embryo.

Character and degree of sexual reversal

The carpellate plants, which are somewhat intermediate from the first, or which sooner or later reverse their sexual expression, produce normal seeds, and some plants were grown from such seeds in the greenhouse. Since the greater part of the development of the individual is complete before anthesis, the carpellate plants continue to appear typically carpellate after reversal except in the floral structures. If partial reversal takes place much before

anthesis, it would be difficult to detect, because the young plants are not so dimorphic as the mature individuals. The time of reversal after anthesis may be at any stage until extreme old age. As stated, some individuals produce only imperfect stamens with defective pollen and indehiscent anthers, while others produce normal staminate flowers with dehiscent anthers and pollen which appears normal in every respect. In such cases the sexual expression usually involves the entire flower, and the perianth is typically staminate, like the perianth on a staminate plant. The reversal from femaleness to maleness is of varying degrees, both as to the perfection of the stamens and the number of flowers produced.

The staminate plants of an intermediate sexual expression are usually so at the beginning of anthesis, few staminate individuals developing carpellate structures at a later stage unless they do so from the beginning. Some, however, continue to be more or less intermediate up to the time of old age and death. If some method of rejuvenation could be employed, it is probable that plants purely staminate at first might be induced to become carpellate later, but under ordinary conditions the change in the staminate plants, as in the carpellate plants, progresses from femaleness to maleness. The reversal in the staminate plants is usually less complete than in the carpellate plants, probably for the reason that senility usually sets in soon after the beginning of anthesis, while in the carpellate plants the long active period after anthesis has begun permits the efficient environmental factors to have full effect in the growing vegetative tissues.

A few special cases were carefully studied in relation to the progressive change in sexual expression. A number of individuals appeared normally carpellate and produced two or three normal seeds, and then gradually changed to the staminate condition, until finally, before they began to die of old age, purely male sex was being expressed. Nothing but typical staminate flowers with dehiscent anthers and normal pollen were being produced. Femaleness had been changed completely to maleness; and this change had taken place in plants which in the seedling stage had been determined as carpellate individuals with decided characters peculiar to the female state. There is but one inevitable rational

conclusion. The decided sexual dimorphism exhibited by the sporophyte of the hemp is not due to some homozygous or heterozygous condition, and is not due to the absence of one or the other sex potentialities. The dimorphism depends on a fundamental state inherent in the cells, either male or female, which can be reversed by the operation of an abnormal environment in the vegetative tissues during the life of the individual. The sexual state is not controlled by segregating Mendelian units. The reversions and transformations are not related to the synaptic associations and segregations of chromosomes in the reduction division, nor in the homozygous or heterozygous mixtures of chromosomes during fertilization. There can be no question that it would be possible with proper environmental control of the original gametes and zygote to determine the original sexual state of the embryo as readily as the established sexual state can be shifted later, either from male to female or from female to male.

In the winter plots a few individuals approached what might be regarded as a monoecious condition. These plants were intermediate in robustness and about as tall as the staminate plants. They developed stamens and gynoecia and abnormal sporophyll structures from the beginning and continued to do so to the end. It is suggested that these individuals were either of a distinct genetic constitution like a typical monoecious plant with the vegetative tissues in a neutral state in respect to sex until the incepts of the flower buds appear, or else the sporophyte embryos were determined as staminate plants of only a slight degree of maleness, and were then reversed to a neutral condition, as in the ordinary types, by the influence of the environment at an early stage, perhaps soon after sprouting. From the neutral meristematic tissue the floral parts would then be thrown either into the male or female state. In cases where a sporophyll is partly staminate and partly carpellate, it must be assumed that the determination of the sexual state was delayed until the tissues were considerably developed, and that then maleness was established at one point and femaleness at another, probably depending on the metabolic level of the cells involved. If the intermediate nature of these plants is due to some definite genetic constitution,

it should be possible to develop a race of hemp which would show monoeciousness under ordinary field conditions. The genetic change from a dioecious to a monoecious condition would be caused by some change in one or more hereditary factors or one or more mutative additions or losses. Such factors, of course, may be present in any number of species, but the point to be emphasized is that such factors or states have no fundamental relation to the sexual nature of the plant, but are only causes which determine more or less definitely at what stage of the ontogeny the sexual state is established. Whether there are special factors in chromosomes for monoeciousness and dioeciousness appears not to be definitely known. In any event, the monosporangiateness or bisporangiateness must not be confused with the sexual state. The one condition or the other simply determines at what stage of the life history a definite sexual state is established, depending on a certain metabolic level, a certain degree of senility of the tissues, or a certain differentiation of the cells. Whether the bisporangiate monoecious and dioecious conditions are due to definite factors or simply to a difference in general constitution, the sexual state in either case could be changed by external causes. There is no fundamental difference between an organism with bisporangiate flowers and one with monoecious flowers as regards sex. The main difference is simply an earlier or later stage of vegetative growth at which the one or the other sexual state is established in a given cell, tissue, or organ. Since it is plain that this is the case, it is not reasonable to suppose that any new principle is involved in passing from a monoecious to a dioecious species, since we know that there is every gradation between bisporangiateness and dioeciousness. The experiments on hemp show that even in a dioecious species with marked dimorphism the male state or the female state is possible in any tissue of a sexual organism, the readiness or difficulty of inducing a change from the one condition to the other depending on various internal and external causes.

Several seeds were obtained from decidedly intermediate plants, but none of them sprouted. This does not necessarily imply any constitutional defect, since many of the seeds from the

dwarfed ordinary carpellate plants are also defective and do not sprout so readily as those grown under normal conditions.

Seeds collected from carpellate plants which later developed stamens were planted in plot 15. There was apparently no difference in the behavior of the plants from these seeds from those raised from seeds obtained from pure parents out of doors, but the number of plants was too small to draw any definite conclusions. One would expect that the embryos of seeds developed under abnormal conditions would show less fixity of the sexual state than those developed under normal conditions. Since practically all the seeds from the out of doors "pure" parents will show reversal of sex with proper abnormal conditions, however, probably the only way to get any definite data indicating a difference would be to test such seeds out of doors in comparison with ordinary seeds. In such an experiment, however, the plants should be grown in an environment which will just keep the plants from normal seeds pure. Such limits can probably be discovered.

Recent work

Various investigators have made observations on the sex ratio of hemp. It is not necessary to refer to the older papers here except to state that a considerable diversity in the proportion of the staminate and carpellate plants has been found. Roughly speaking, the ratio of carpellate to staminate plants is 1:1, with a deviation in either direction of at least 50 per cent in extreme cases, even when large numbers are counted.

In 1916 PRICHARD (2) published his results on changing the sex in hemp by mutilation. By removal of leaves and flowers, and by certain other treatments, he was able to obtain 17.8 per cent of reversals in the established sexual state. In all, 25 carpellate and 4 staminate plants showed reversal of sex.

YAMPOLSKY (7), working with *Mercurialis annua* L., found that some carpellate plants produced staminate flowers and some staminate plants produced carpellate flowers, and that both staminate and carpellate plants showed gradations in degree of maleness and femaleness. He also found that the offspring of

selfed carpellate plants are carpellate or prevailingly carpellate, and the offspring of staminate plants are staminate or prevailingly staminate. This condition is probably what should be expected if the seedlings are grown in the same environment as the parents. It would be interesting to know whether this condition could be modified by raising the seedlings in a fundamentally different environment. The writer knows from experience, however, that *Mercurialis* is a much less satisfactory plant for study than hemp, because of its minute flowers, less prominent dimorphism, difficulty of gathering seed, etc. YAMPOLSKY (**8**) also found flowers with confused sexual expression much like what is reported in this paper for hemp. He rightly concludes that "a factorial hypothesis of sex cannot explain these results," that is, the periodic alternation of sex in the course of the plant's development.

I have already shown (**3**) the significance of the change in the sexual state of a bisporangiate flower, taking as examples the cones of a *Selaginella* and the flowers of a *Bromus*, and showing that the establishment of the sexual state in the organs involved had nothing to do with a Mendelian segregation depending on the synapsis and segregation of chromosomes.

STOUT (**6**) has made a study of intersexuality in *Plantago lanceolata*, and found that there is a wide range of variation in the degree in which maleness is expressed. He also found that femaleness varies in the degree of its expression.

DAVEY and GIBSON (**1**) found that the changes in the sexual state, which they studied in *Myrica Gale*, were in some way associated with environmental conditions. The relative proportion of carpellate plants was found to be greater in the wet than in the dry areas. *Myrica Cale* would probably be a desirable perennial species for experiments on the environmental control of the sexual state, as the hemp is for a short-lived annual.

The writer (**4**), while studying the intermediate plants of *Morus alba*, found a staminate tree that had one large reversed lateral branch and a second small one at the top. These branches were bearing fruit, but although they were decidedly carpellate, they were so only to a degree, for both were still producing staminate catkins. The seeds of this fruit were perfectly normal, and the

writer now has a progeny of young trees from this "male individual." This reversal of the sexual state took place in the meristematic tissue of the staminate sporophyte. A state which in general always causes the expression of male characters through some internal cause was changed to a new sexual state or a neutral condition by which the sexual expression in the incipient aments was easily thrown into the female or the male state, while the rest of the tree, consisting of numerous large branches, was in such a sexual state that maleness was invariably expressed in the incipient aments. This tree functions the same from year to year. All such cases, as well as the remarkable behavior of hemp, show that a Mendelian hypothesis of sex is at present not only untenable, but is absurd in the extreme. It is not even necessary to have such a hypothesis as an explanation of sex in the higher animals in which the nuclei of the two sexes show an allosome difference.

I have stated (3) that the great abundance of intermediates among the winter hemp plants was probably due to the abnormal environment, mainly a lack of light. The statement was also made that hemp was "a dioecious plant which shows sexual dimorphism even in its remote vegetative parts, but numerous individuals which are thus specialized have the ability to produce the opposite primary sexual generation and sexual cells, without any manipulation whatever being employed, except that they were grown in an unusual environment." It behooves the advocates of the hypothesis of homozygous and heterozygous constitutions to show how their hypothesis works in these numerous examples now on record before attempting to confuse biological literature with an apparently untenable theory. The present work on hemp shows that the attempt to analyze the sexual constitution of monosporangiate or bisporangiate plants from ratios which appear in cultures is of little value unless it has previously been shown that the plant reacts the same to all environments. In any dioecious species which has sex intergrades, and there are apparently few which do not have them, it is of no genetic importance to discover that a certain "pedigreed" individual has produced so many "males," "females," and "hermaphrodites," unless it is definitely known that the same kind of seeds would not give a different progeny if

grown in an entirely different environment. Sex goes beyond the organized visible structure of the protoplasm, and is probably bound up with the atomic or molecular structure, or dependent on some physical state which is reversible in most cells. It seems impossible to explain the known facts of sexuality and sexual morphology by any activities or movements of the larger structural units of the protoplast, such as chromosomes, chromatin granules, centrosomes, nucleoli, chondriosomes, etc.

The geneticist must give as much attention to the expression of heredity as to the analysis of hereditary factors, and it is becoming more and more apparent that the environment plays a very prominent part in such expression, the characteristics of the individual being decidedly different when developed under one environment from what they would be if developed under another. So far as sexuality is concerned, the cells may be in such a state of equilibrium that closely associated groups may be thrown into the opposite sexual state and be differentiated as such simply because the one area is at a different metabolic level from the other. It is a common occurrence, therefore, not only in hemp but in great numbers of species, for sporophylls to be microsporangiate in one part and megasporangiate in another, or to have the characters peculiar to maleness in one part and those peculiar to femaleness in the other.

Hemp is recommended as perhaps the most convenient plant to grow for experimental purposes, for classes in genetics, and to illustrate confusion of sexual expression and sex reversal. The flowers appear in from 30 to 36 days if planted about December 10, and the staminate plants can mostly be studied before it is necessary to pay attention to the carpellate individuals. The extreme dimorphism, the lack of vestigial parts in the normal flowers of the opposite set of sporophylls, the response in size of the plant at various seasons, and other peculiarities combine to make hemp of unusual interest to the student.

The writer is under obligations to Mrs. BAYARD TAYLOR for much assistance in the work on plots 8, 9, 13, and 14; and to Mr. R. J. SIM for assistance in the illustrations.

Summary

1. Hemp planted in spring in the open, under normal conditions, developed as pure carpellate and pure staminate individuals. There is no confusion of sexuality.

2. The ratio between carpellate and staminate individuals is about 1:1, with a large deviation in either direction for various plots.

3. Hemp planted in winter in the greenhouse on shallow benches with low light intensity showed great confusion in sexual expression. Abundant irregularities were produced, such as stamens with normal stigmas and structures partly carpellate and partly staminate, as well as more typically bisporangiate flowers and flowers typical of the opposite sexual state.

4. Both carpellate and staminate plants showed reversal in their growing period to the opposite sexual state.

5. In extreme cases 88+ per cent of carpellate plants showed reversal to maleness, and 80 per cent of staminate plants showed reversal to femaleness.

6. Both staminate and carpellate plants, although they showed decided sexual dimorphism, contained all the factors and abilities of both sexes. There is no question of a homozygous or heterozygous condition involved. The staminate and carpellate individuals contain the potentialities for the perfect development of the opposite sex. Reversal of the sexual state takes place in the vegetative tissues, and has no relation to a reduction or segregation of chromosomes or their possible hereditary factors.

7. The sexual reversal is of all degrees of intensity, from very imperfect expressions of the opposite organs to completely normal development.

8. Sexuality is a state or condition not Mendelian in nature, but related to the functional activity of the plant and profoundly influenced by environment. Maleness and femaleness in hemp are probably controlled by the metabolic level of the cells, and sex reversal takes place when the metabolic level is decidedly changed or disturbed.

9. Any tissue in its growth may be in a neutral state of varying degrees of intensity, and during its continued growth can pass

from one state to the other without any reference to chromosome segregation or combination which are the ordinary causes of Mendelian phenomena.

10. Sex is subject to experimental control in the individual in such dimorphic, dioecious species as hemp, and such control can be exercised in various ways by changing the ordinary factors of environment, and, therefore, presumably also by chemical and physical stimuli of various kinds.

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EXPLANATION OF PLATE XI

All the figures are slightly magnified.

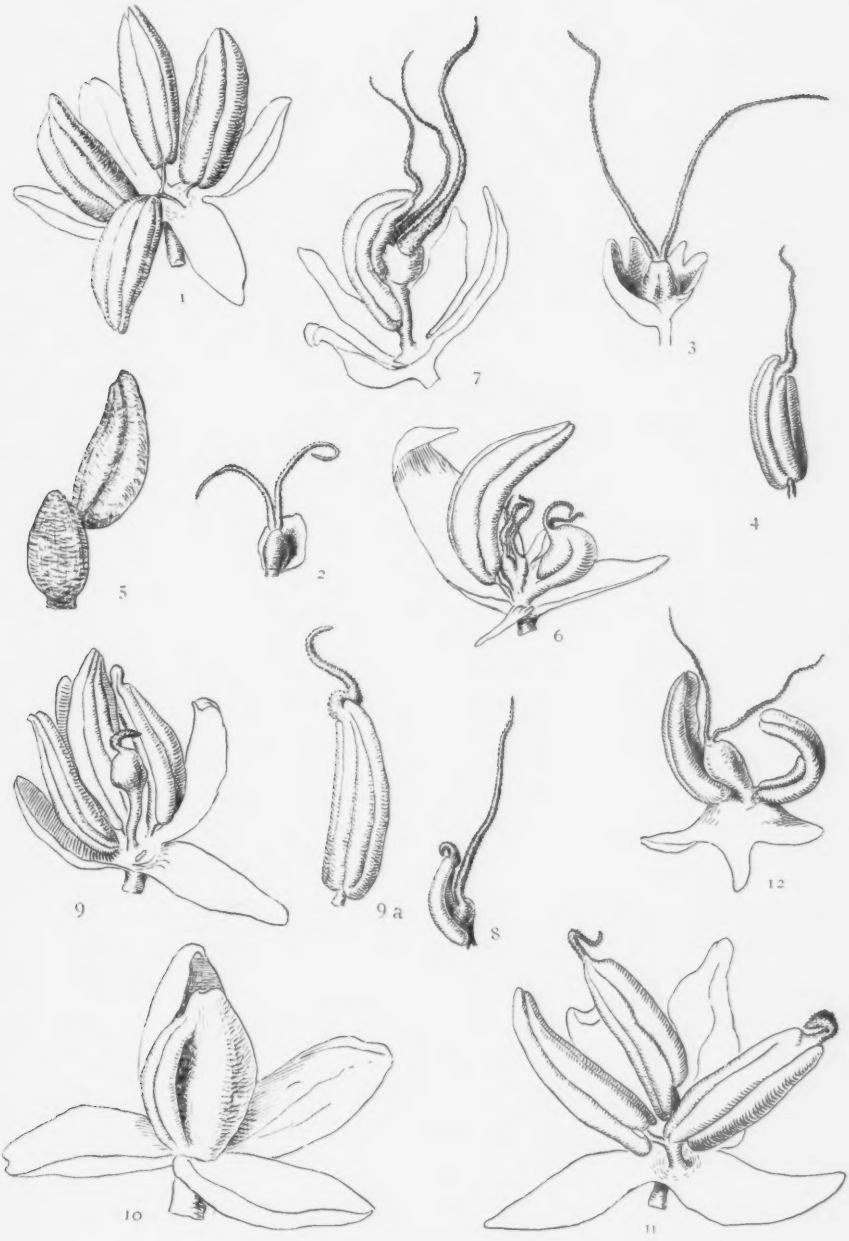
FIG. 1.—Normal staminate flower from staminate plant just before dehiscence of anthers.

FIG. 2.—Normal carpellate flower from carpellate plant; perianth is sheath with oblique limb; sheath or calyx cut open to expose ovulary.

FIG. 3.—Nearly perfect carpellate flower from base of staminate inflorescence on staminate plant; 4 sepals fused together; side of calyx torn open to expose ovulary; in staminate plants usually most perfect carpellate flowers develop first.

FIG. 4.—Stamen with stigma; from staminate plant.

FIG. 5.—Ovulary from carpellate plant with stamen growing from one side; ovulary is flat on side from which anther projects.



SCHAFFNER on HEMP

FIG. 6.—Distorted flower from tip of inflorescence of carpellate plant, with 1 good stamen and 1 reduced and distorted stamen with 2 stigmas connected at base with double structure halfway between anther and ovulary in character, having 3 stigmas; stamen side of flower has sepal of normal size; such perianths often staminate in character on one side and more or less carpellate on other.

FIG. 7.—Abnormal flower from same carpellate plant as fig. 6, showing distorted stamen with stigma and distorted ovulary with 2 stigmas, all on central stalk; 4 sepals.

FIG. 8.—Stamen-carpel complex from center of staminate flower, from staminate plant; 4 normal stamens present; bilocular stamen ends in short filament and imperfect ovulary has 1 prominent stigma.

FIGS. 9. and 9*a*.—Distorted staminate flower from staminate plant with stalked rudimentary gynoecium ending in small stigma and with 4 stamens; 2 stamens normal, one has projection like incipient stigma, and one (fig. 9*a*) has prominent stigma; 4 sepals.

FIG. 10.—Tip flower from inflorescence of carpellate plant showing 4 free sepals characteristic of staminate flower and one side of ovulary developed into anther-like structure with imperfect microsporangia.

FIG. 11.—Staminate flower from carpellate plant; 3 stamens on stalk in center of flower, 2 having small stigmas; 4 sepals.

FIG. 12.—Abnormal flower from staminate plant expressing femaleness; abnormal ovulary with 2 stigmas united with 1 anther not normally developed; on anther side perianth sheath has 3 lobes and is thus somewhat carpellate in nature; other stamen normal; sheath split open and turned down to expose ovulary.

EXPERIMENTAL INVESTIGATIONS ON BIRCH AND OAK[1]

EDITH S. WHITAKER

(WITH PLATES XII–XV AND FOUR FIGURES)

At the present time experimental investigations have a well merited vogue, especially in genetical and morphological fields. Until recently, however, little has been done in this connection on the structure of woody plants. This has been due largely to the fact that the history of woody plants has not been sufficiently understood to warrant their interpretation. The doctrine of evolution was formulated mainly through the study of comparative anatomy in the absence of a fossil record. Plant tissues, however, are more resistant to decay than animal tissues (with the exception of bones), and as a consequence their historical relations and affinities have become available for comparison with existing forms and structures. The comparative anatomical study of existing and fossil plants has led to the conclusion that there are certain general principles which not only hold true for a group of plants in which there is a fossil record, but also may be applied to other groups in which, as in the Angiosperms, there is as yet no complete geological record. Certain general conclusions thus inductively established make it possible to apply the same principles in judging anatomical features and interpreting structural relationships in the Angiosperms, in absence of fossil record (**4**, **5**, **7**).

The first principle established as a result of comparative anatomical study and knowledge of fossil forms, and one employed by zoölogists, is based on the fact that in the course of their development organisms may pass through conditions now lost in adult life, but once possessed by the organism in its mature state. This is called the law of recapitulation, and holds true in plants also. For example, certain of the Cupressineae which have small leaves in the adult plant, in their seedling development have the larger leaves characteristic of the more ancient flora.

[1] Contribution from the Laboratories of Plant Morphology of Harvard University.

A comparative anatomical study of existing and fossil plants, especially the Gymnosperms, has shown that certain parts of plants (as the root, leaf, first annual ring, and reproductive axis) may have a different organization of tissues from the stem, which is more highly specialized. This fact has been responsible for the theory of retention, or, as it has been more recently called, the doctrine of conservative organs (7).

The third principle is based on the fact that upon injury certain structures and types of organization appear which are characteristic of older forms and more conservative regions of the plant. It is less well understood than the other two, and is capable of more misinterpretation. It is the one of chief interest in the present investigation. It should be pointed out, however, that only those structures occurring as a result of wounding which are comparable to conditions presented by the seedling and the conservative organs (root, leaf, etc.) can be relied upon in the interpretation of wound reactions.

Experimental work on woody tissues is of interest not only from a general biological standpoint, but is also of importance from the point of view of plant pathology. It may be pointed out also that such investigations are of interest from an economic point of view, since they suggest the possibility of producing experimentally valuable ornamental woods.

As the subject of wound reactions is a large and complicated one, for the purposes of brevity and clearness I have confined myself to those traumatic features which are connected with ray structures only. Other reversions and reactions consequent upon injury in the birch and oak, therefore, may be conveniently postponed until a later date.

Ray organization in Angiosperms

The three types of broad rays characteristic of the angiospermous forest trees are all found in different species of the isolated and probably ancient genus *Casuarina*. A synoptic diagram illustrating these types as seen in *Casuarina* is given in text fig. 1. The simple or uniseriate ray which is a feature of the wood organization of the Conifers is also found in Angiosperms, and its occurrence

need only be noted in the present connection. In the center of text fig. 1 is the type of ray known as the aggregate ray (A, A'). This is a radial band composed of congeries of small or uniseriate rays and clusters of fibers. The leaf trace is represented in solid black at the interior of the segment. The aggregate ray originated probably in the clustering of uniseriate rays around the outgoing leaf trace, and seems to be the most ancient type of broad ray found in forest trees. It is found in the root and seedling stem of

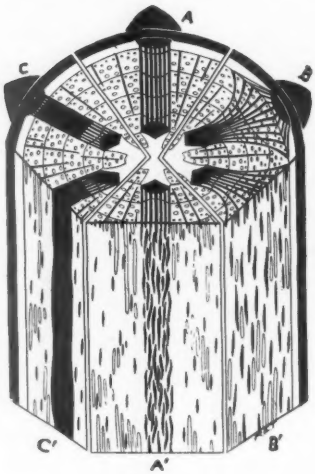


FIG. 1

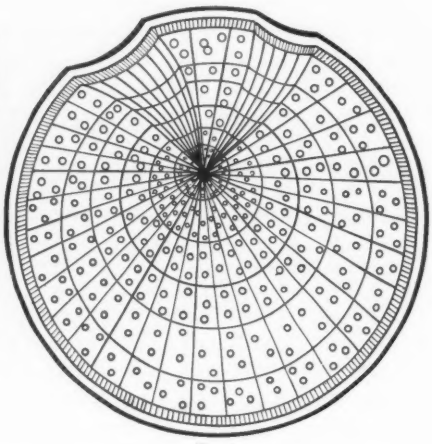


FIG. 2

FIGS. 1, 2.—Fig. 1, synoptic diagram illustrating ray situation in *Casuarina;* fig. 2, diagram of birch root.

Casuarina, and persists in the adult axis of *C. torulosa*. It is also characteristic of the adult stem wood of the alder and of the southern oaks.

The second type of angiospermous ray, represented at the left of the diagram, is known as the compound ray. It is found in *Casuarina Fraseri*, in the mature axes of oaks of northern range, and in herbaceous Dicotyledons. Immediately outside of and subtending the leaf trace (black) is the aggregate condition already mentioned. Farther out toward the periphery of the stele, however, the fibrous parts of the ray have undergone a parenchymatous

metamorphosis. The homogeneous character of the ray is indicated by solid black. The depressions of the cylinder, corresponding in position to the large rays in the vicinity of the annual ring, are to be noted.

The type of ray characteristic of the majority of our forest trees is the diffuse ray. The organization of this is shown at the right (*B*, *B'*). Just outside the leaf trace (black) the ray is characteristically aggregate, a situation parallel to that of the early organization of the compound ray. Farther out, however, the rays spread out and subdivide, instead of being more closely united, and vessels and fibers again appear in the foliar segment. This permits the passage of more water and food substance, and is of advantage to trees subject to the rigors of a northern winter. In tangential aspect the rays are several cells wide, which differentiates them from the simple or uniseriate rays of the Conifers. This type of ray is found in the mature stem of *C. stricta* and *C. equisetifolia*.

Ray organization in birch and oak

BIRCH.—Fig. 1 represents a transverse section through the stem wood of *Betula nigra*, and shows the type of ray characteristic of most of our forest trees. Fig. 2 shows some of these diffuse rays in tangential aspect. They are about three or four cells in width, but without any interspersed fibers. It is an interesting fact that most birches of southern origin or affinity retain the aggregate type of ray organization in their vegetative axes, while those of northern range are characterized by the diffuse type of ray. *B. populifolia*, for instance, which is essentially a southern birch, has persistent aggregate rays in the normal stem wood. *B. pumila* and *B. lutea* may be taken as examples of the northern species. This difference in ray organization would seem to indicate the evolutionary relationships occurring in response to weather exigencies.

B. alba, an introduced and also indigenous species, may be taken as an example of a birch belonging to the temperate region, and will be used in this investigation because of its intermediate position geographically and structurally, where no special advantage is to be gained by recourse to other species.

OAK.—The oak is the outstanding arboreal form with compound rays. It is this that makes oak wood in great demand for building purposes. The northern oaks show the compound type of ray structure, while on the other hand the southern oaks retain the aggregate type of organization in the mature stem wood. Discoveries of fossil oaks (1, 2) from the gold gravels of California (Miocene) indicate that the aggregate condition was the general one in previous geological epochs. Hence on the basis of comparative anatomy and of geological record the aggregate ray seems to be the primitive one for the oak.

The compound ray was apparently an evolutionary response to the demands of a rigorous winter and to the need of storing up food in abundance. The fact, observable on any hillside in winter, that the oaks of northern latitudes, particularly the seedlings or saplings, retain their leaves late into the winter is an interesting evidence of their southern derivation. The older trees gradually become early deciduous.

Fig. 3 shows a transverse section of a stem of *Quercus rubra*. In the center is a compound ray, composed undoubtedly of homogeneous cells from which vessels and fibers are conspicuously absent. Fig. 4 shows some of these compound rays of the same species in tangential aspect. These may advantageously be compared with the tangential view of the aggregate rays of the birch as shown in fig. 2.

Birch

WOUNDED STEMS.—Fig. 5 represents the polished disk of a wounded birch log, in which the wound has become so nearly healed that it appears far on the inside of the stem, and would not be discernible from the outside. The return to apparent normal conditions of growth is often very complete in the birch, and bark forms again on the outside. It also occasionally happens that bark grows over wounds of such large extent that the two edges of the injury have not grown together. This region of overgrowth or hypertrophy is known as the wound cap, and is represented at the top of the figure, above the wound. It may be noted in this connection that growth on the side of the stem which has

been wounded has been more rapid than on the lower side where there has been no disturbing influence.

The place in which reversionary structures make their appearance (in this case the aggregate rays) is usually not in the region of the wound nor yet in the wound cap, but in the region of slower growth opposite the wound. This fact will be more apparent when the microscopic features are discussed.

ROOT AND VEGETATIVE STEM OF B. NIGRA.—One of the most conservative organs of a plant is the root. Fig. 7 is a transverse section of a root of *B. nigra* showing two rays related to root traces. That these rays are aggregate in organization, and not diffuse, as are the leaf rays of the stem in figs. 1 and 2, may be seen by referring to a still higher magnification of these rays in fig. 8. Taking the root as an organ in which primitive features are long retained after they have been lost in the vegetative axis, it would seem that the aggregate ray is the primitive one for *B. nigra*.

Another conservative region is the node of the stem, and ancestral features are often found here in connection with the leaf ray. Fig. 9 shows a part of such a stem in this critical region in transverse section of *B. nigra*. Although the normal adult stem is characterized by diffuse rays, the aggregate type of organization is present in the first formed annual ring, itself a conservative region.

ROOT, SEEDLING, AND REPRODUCTIVE AXIS OF B. ALBA.—Passing from a species with typically diffuse rays, even in the reproductive axis, it is of interest to note the ray organization in significant regions of *B. alba*. As stated, the root which longest retains the older type of ray structure shows such a close resemblance to that of *B. nigra* in important anatomical features that for comparative purposes fig. 7 will illustrate the situation found in the root of *B. alba* sufficiently well. In both the ray organization is aggregate.

Fig. 10 represents a seedling of *B. alba* in transverse aspect, and even under low power the ray structure may be noted as aggregate. A higher magnification to show the detailed organization of one of the rays is not necessary, as they are anatomically similar to that shown in fig. 12 (a leaf ray through the reproductive stem of the same species). Fig. 11 is a low power magnification of a reproductive axis of *B. alba*. Here the decided aggregation of rays in

the foliar segment is a marked feature of the woody cylinder, in connection with contrast with that shown in fig. 9 for *B. nigra*. Fig. 12 shows one of these aggregate rays under a higher magnification.

Since the root, seedling, and reproductive axis of *B. alba* show the presence of aggregate rays, it may be assumed, on the basis of principles derived from the study of living and extinct Gymnosperms, etc., that the aggregate condition is the primitive or ancestral one in these species. This interpretation will be used in the present connection for determining the traumatic responses in wounded stems.

WOUNDED STEMS OF B. ALBA.—Fig. 13 represents a transverse section made through a wounded vegetative axis of *B. alba*. The marked acceleration in growth in the wound cap which appears at the top is to be noted, as well as the corresponding retarding on the opposite side. Even under low power the flutings in the annual rings formed after injury may be seen on the side of the stem away from or opposite the wound. These crenulations represent aggregate rays, which are not present in the normal wood, and mark the position where reversionary or traumatic features appear in wounded birch stems. The excessive hypertrophy which is so marked a characteristic of wounded birch stems does not seem to be favorable to reversion, since only diffuse rays are found in the wound cap itself. Fig. 14 is a tangential section through the region opposite the wound of the stem figured in fig. 13. The undoubtedly aggregate nature of the rays is evident. Fig. 15 shows some of these rays under a higher magnification, and the aggregation of rays and fibers is even more apparent.

WOUNDED SEEDLING OF B. PAPYRIFERA.—A species closely allied to *B. alba*, and having the normal wood structure of northern birches is *B. papyrifera*. Fig. 16 represents a transverse view of a wounded seedling of this species. The region where reversionary structures might be expected to occur is opposite the wound (*X*). Fig. 17 illustrates the condition in the immediate region of the hypertrophy. This is typical of the region of the wound cap in the birches in general. The ray organization in this instance is undoubtedly diffuse, and similar to that shown in the case of the normal stem wood of *B. nigra* (fig. 1).

Fig. 18 is a higher magnification of part of the region indicated by *X*, and is in decided contrast with fig. 17 in ray structure. Here the rays are aggregate in organization at the outer edge of the stem, in that part of the wood laid down after the stem had been wounded. The central part of the stem shows only diffuse rays similar to those in fig. 17. These aggregate rays are true reversions, and the place at which they appear (opposite the wound) is significant for the birches.

WOUNDED SEEDLING OF B. POPULIFOLIA.—Since aggregate rays are present as a typical feature of the normal stem wood of *B. populifolia*, it might be expected that they would die out in the region of the wound. This is precisely what does happen. Farther back, laterally, they make their appearance in the cylinder but not as traumatic features.

SUMMARY.—Text fig. 2 represents diagrammatically the ray situation obtaining in the root of *B. alba*, and of the genus as well. In the Betulaceae the aggregate type of ray is found universally in the root, essentially a conservative organ. This ray is in definite relation to the root traces, and is the primitive or ancestral type of ray for the genus.

Text fig. 3 represents a wounded stem of *B. alba*, and shows the comparative acceleration in growth of the wound cap and the rest of the cylinder. No aggregate rays appear in this region of marked hypertrophy. The reversionary structures appear opposite or behind the wound, on either side of the stem, and extend in some instances to the extreme opposite side of the woody axis. The seedling condition is represented in the central part of the figure, the aggregate rays appearing in connection with the foliar segment. The leaf gap is shown in black. The aggregate rays related to the foliar segment persist only through two or three annual rings, and then gradually become diffuse, the diffusion taking place first on the sides of the rays. The reproductive axis is also figured in connection with the foliar segments by supposing that the aggregation does not give way to the diffuse type of ray as in the seedling, but continues aggregate out into the cortex.

CONCLUSIONS.—That the aggregate ray is the primitive one for the birches is borne out by the fact that it is the type of ray

organization that persists in the roots of all species of the genus. The aggregate ray is also found in the reproductive axes of certain species, notably *B. alba*. It appears in the seedling in the mature stem of southern species, and as a result of injury when not normally present in the stem. *B. nigra*, which has diffuse rays in the stem, recalls the aggregate type upon injury to the vegetative axis, and shows an aggregation normally in connection with the root trace. *B. papyrifera*, a northern species, recalls aggregate rays in

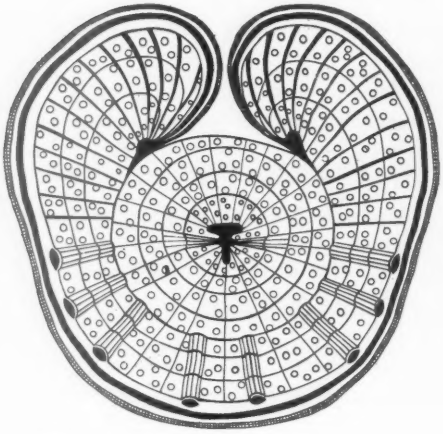


FIG. 3

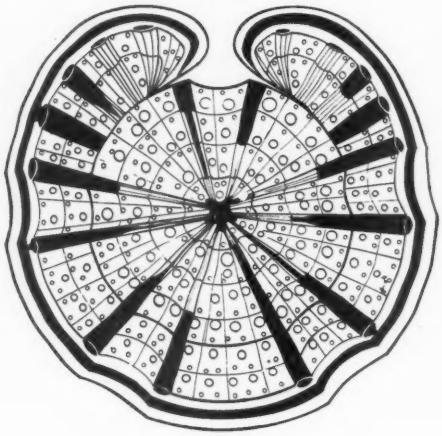


FIG. 4

FIGS. 3, 4.—Fig. 3, diagram of wounded birch stem, showing relations and positions of traumatic features; fig. 4, diagram of oak stem, showing seedling condition and traumatic behavior of ray structures.

the seedling as a consequence of injury. Traumatic reactions should be interpreted in the light of data gained from the organization of conservative regions, etc.

Reactions occurring in the wound cap are the result of hypertrophy and are not to be considered as reversions, since they are not correlated with structures that are known from their distribution in the seedling and conservative regions to be primitive. True reversions in the birch, as exemplified in this investigation by *B. alba* and *B. papyrifera*, occur opposite the wound and not in the wound cap. *B. populifolia*, which has aggregate rays in the

normal wood, loses them as a result of wounding except in connection with the appendage, when they may appear in the wound cap.

Abies

It will be helpful to summarize the wound reaction situation in Conifers. From the point of view of wound reactions two features are significant, resin canals and ray tracheids. The Abieteae show a simplification or reduction of wood organization in lacking both of these characters in the normal wood (3). The root, however, has resin canals as a normal feature of its structure.

In *Abies*, which has neither resin canals nor marginal ray tracheids in the normal stem wood, the situation in regard to reversion is interesting, because both resin canals and ray tracheids are recalled as a result of injury. There is a significant feature, however, in connection with the reappearance of these traumatic characters which parallels the situation obtaining in the angiospermous groups under consideration. It has been pointed out by THOMPSON (8) that marginal ray tracheids which are not normally present in the fir may be recalled as a consequence of injury, and that reversion takes place opposite the wound. JEFFREY (6) had earlier shown that in the case of a wounded stem of *Cunninghamia sinensis* marginal ray tracheids, which are not a feature of normal stem organization, are recalled, and that these make their appearance opposite the wounded region.

The appearance of traumatic resin canals as a result of injury is of special interest from the fact that they do not reappear in the region opposite the wound, as do the marginal tracheids, but in the wound cap itself. This condition, as will be evident later, parallels the situation in *Quercus* in connection with reversionary ray structures.

Oak

WOUNDED STEMS.—Fig. 6 represents the polished end of a wounded oak log *Q. rubra*. In this instance the healing has not been so complete as it was in the birch, and therefore the wound cap is restricted to the sides of the actual injury. This would be expected as a result of the slow growth of the oak, and accordingly reversionary structures will be expected in the wound cap itself, and

not in the region opposite. Thus it is seen that the place at which reversionary structures occur depends on the localization and nature of the hypertrophy.

ROOT OF Q. RUBRA.—The ray structure of the roots of northern oaks is aggregate. Fig. 19 shows a transverse section of a root of *Q. rubra* in which the aggregate nature of the rays is apparent. The details of the aggregation may be seen to better advantage in fig. 20, which represents one of these rays under higher magnification. In the central part of the ray the organization is more parenchymatous than on the outer edges. The aggregate condition persists in the roots of the most mature trees, and is good evidence that the ancestral type of oak ray is aggregate, if it be admitted that the root more than any other organ longest retains primitive features.

Fig. 21 is a tangential section through a root of *Q. rubra*, and the undoubtedly aggregate condition that it presents may be compared with the tangential aspect of ray organization in the stem as represented in fig. 4.

SEEDLING.—The oak seedling in its younger stages has clearly developed aggregate rays. In the older saplings the aggregation may be noted in the first formed annual rings. In the successive annual rings the aggregate type passes over into the compound ray. No separate illustration of this is given because it resembles so nearly that described for the root. Seedlings of *Q. rubra*, *Q. velutina*, and *Q. alba* all show aggregate rays, so it may be assumed that it is a general situation for the genus.

REPRODUCTIVE AXIS.—The reproductive axis of the oak does not show aggregate rays. They have disappeared in the genus probably because there is no longer any definite localization of the acorn-bearing branches, as in the ovuliferous aments of birches. Species of oak of extra-tropical range have in general lost the catkin-bearing habit (in the case of the female flowers).

STEM.—The situation in the oak regarding wounding is somewhat different from that of the birch. The recovery from injury is much slower, and the conditions of atrophy are more marked in the region of the wound than those of hypertrophy. Aggregate rays (1), similar to those figured as normal in the root and seedling,

however, appear in response to a mechanical stimulus, as in the birch.

Fig. 22 represents a transverse section of a wounded stem of *Q. velutina*. The extent of the wound is considerable, and healing has taken place to a comparatively small degree. The wound cap is restricted as a consequence to the edges of the wound, and it is here that reversionary structures make their appearance. The immediate region of the wound cap blots out all large rays, but directly behind this laterally the rays become aggregate, and finally compound again as they approach the back of the stem. Fig. 23 shows some of the rays in the wound cap of fig. 22 under higher magnification. Here the aggregate nature of the rays is quite apparent, especially if it be compared with that showing a typical compound ray (fig. 3). In the immediate vicinity of the wound the rays are all small, and in tangential section appear similar to the diffuse rays of the birch. If one were to interpret conditions here as being reversions, with no reference to the other parts of the stem or to conservative regions, he would have to postulate the diffuse ray as the primitive one for the oak, a situation which is in no wise borne out by the facts of the case, as in neither fossil forms nor in conservative regions of existing species are diffuse rays found. This illustrates the danger of judging traumatic features on their face value without regard to other organs or to the past history of the plant. Only those structures occurring as a result of wounding which can be shown to be characteristic of southern and fossil forms, or of the seedling or conservative regions, can be accepted as significant in connection with wounding in the northern species.

Fig. 24 represents under fairly high magnification a traumatic wood ray of *Q. velutina* in transverse section. It is also illustrative of the manner in which the aggregate ray of the seedling becomes compounded in the older saplings.

It is of interest to note in connection with wound reactions that oak galls produce a return to aggregate condition similar to that ensuing when a stem is wounded in any other way. The organization of the gall itself is complicated, and need not be considered in the present connection.

SUMMARY.—The general situation obtaining in seedling oaks and wounded stems may be seen by referring to text fig. 4, which is a schematic representation of a wounded oak stem, and illustrates the position of reversionary features on the edge of the wound cap. These reversionary rays are represented by a series of parallel lines, in contrast with the compound rays, which are solid black. Traumatic aggregate rays occur in the wound cap itself, and laterally they pass over into the normal compound type. A comparison with text fig. 3, representing a wounded birch stem, brings out the important difference in respect to wound reaction and the position of traumatic features in *Betula* and *Quercus*. The transition from aggregate to compound ray in the seedling stem is shown in the center, in which the compound character of the ray is represented in solid black as the ray approaches the periphery of the stem.

CONCLUSIONS.—The northern oaks in their vegetative axes have the compound type of ray typical of the herbaceous forms. On the other hand, the southern oaks have aggregate rays in the adult stem, and fossil representatives of the genus are likewise characterized by the presence of aggregate rays. The seedling and the root of living northern species possess aggregate rays. There is no special localization of the reproductive branches in the oak as in the amentiferous forms like the birch. This region, therefore, which is ordinarily of importance in connection with the determination of primitive structure, is of no value here.

Wounding brings back aggregate rays in the adult axis, and in the older seedlings which have begun to form compound rays. The results of injury here, as in the birch, must be interpreted with reference to the nature and extent of the wound. The wound cap of the oak is much smaller than that of the birch, and does not so often show hypertrophy to any marked extent. Reversionary structures accordingly appear on the edge of the wound in the wound cap proper, slightly behind the immediate region of injury. Oak galls stimulate reversion to an aggregate type of ray structure.

Summary

1. Experimental investigations are of interest in connection with woody plants both from a general biological point of view,

and also from the standpoint of plant pathology. They are also of interest because they suggest the possibility of producing ornamental woods experimentally.

2. Three types of rays, aggregate, compound, and diffuse, which persist contemporaneously in *Casuarina*, are characteristic of angiospermous trees. The aggregate seems to be the more primitive one, from which the diffuse and compound have been derived by different processes of evolution.

3. Wound reactions in woody forms must be considered with reference to the conservative regions, the seedling structures, and fossil record, because only those structures occurring as a consequence of injury which have parallel conditions in these parts can be regarded as true reversions.

4. Work on living and extinct Gymnosperms has established certain principles on the basis of which experimental investigations in angiospermous woods may proceed a priori.

5. All reactions following wounding are not true reversions. In general extreme hypertrophy is not favorable to reversion.

6. The details of wound reaction in the birch and oak are different. In the birch the wound cap is large, the hypertrophy being very marked. As a consequence the traumatic or reversionary features are not found in this region, but in that part of the cylinder opposite the wound.

7. *Abies* recalls marginal ray tracheids as a consequence of wounding. These are found in the regions remote from the wound and parallel the situation obtaining in the birch. On the other hand, the mode of appearance of traumatic resin canals is similar to that of the aggregate rays resulting from injury to northern oaks, as the reversionary resin canals occur in the immediate region of the wound cap.

8. In the oaks the wound cap is small and does not show hypertrophy to any marked extent. Correlated with this, reversionary features appear in the wound cap proper, in contrast to the birches.

In conclusion, I wish to thank Professor E. C. Jeffrey, under whose direction this investigation has been made, for advice, material, and the use of text fig. 1 from his recent book, *The Anatomy of Woody Plants;* also my father for assistance in securing material.

Harvard University

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EXPLANATION OF PLATES XII–XV

PLATE XII

FIG. 1.—Transverse section of normal stem wood of *Betula nigra*, showing diffuse rays.

FIG. 2.—Tangential view of same.

FIG. 3.—Transverse section of normal stem of *Quercus rubra*, showing compound ray.

FIG. 4.—Longitudinal section of same, showing compound ray in tangential aspect.

FIG. 5.—Transverse view of wounded stem of *Betula alba*.

FIG. 6.—Transverse section of wounded stem of *Quercus rubra*.

PLATE XIII

FIG. 7.—Transverse section of root of *Betula nigra*.

FIG. 8.—Part of same more highly magnified to show aggregate ray.

FIG. 9.—Transverse section through nodal region of *B. nigra*, showing one of leaf traces.

FIG. 10.—Transverse section of seedling stem of *B. alba*.

FIG. 11.—Transverse section of reproductive axis of *B. alba*.

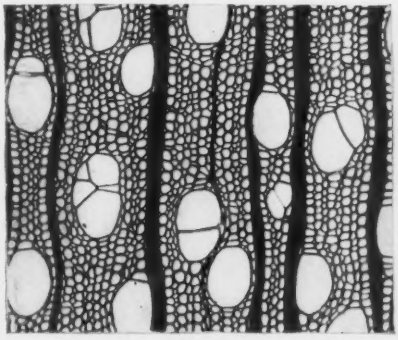
FIG. 12.—Part of same more highly magnified.

PLATE XIV

FIG. 13.—Transverse section of wounded stem of *Betula alba*.

FIG. 14.—Tangential section through region opposite wound in stem of *B. alba*.

FIG. 15.—Part of same more highly magnified to show aggregate character of rays.



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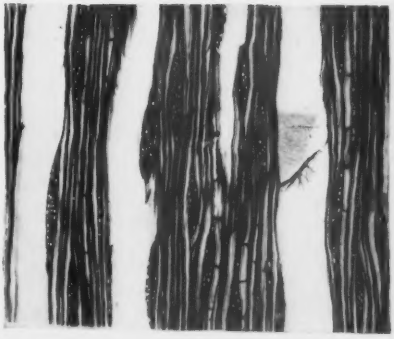

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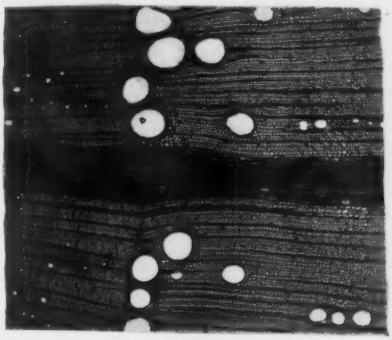

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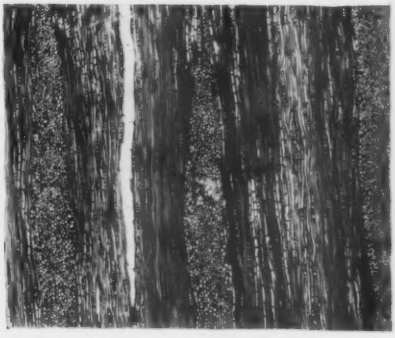

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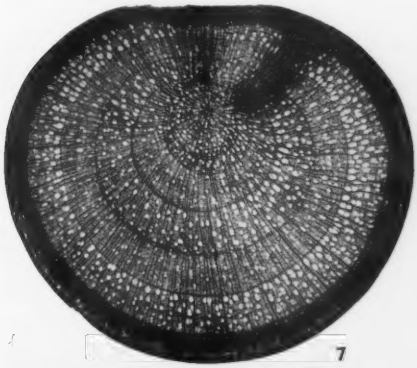
WHITAKER on BIRCH and OAK



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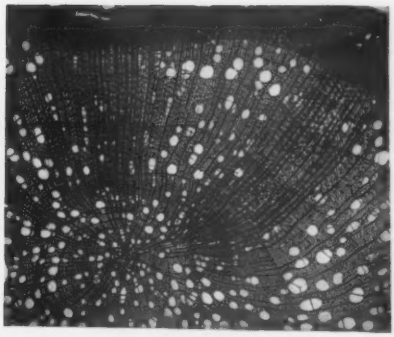

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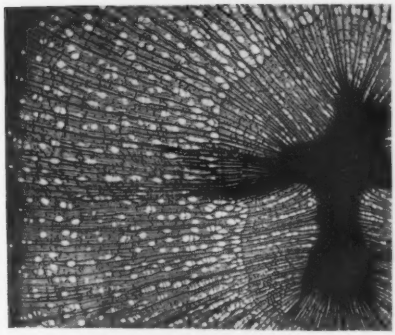

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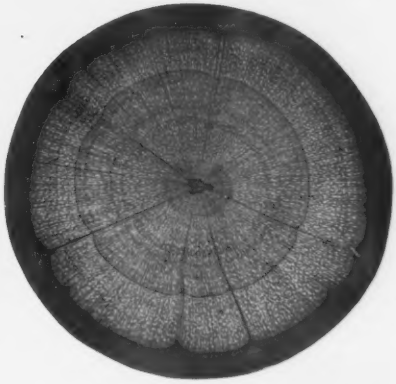

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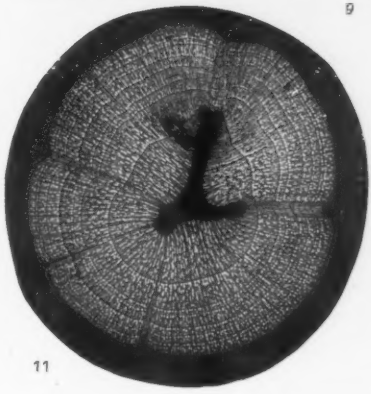

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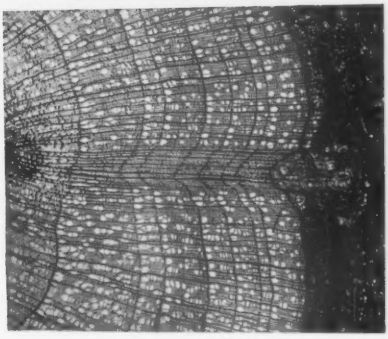

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WHITAKER on BIRCH and OAK

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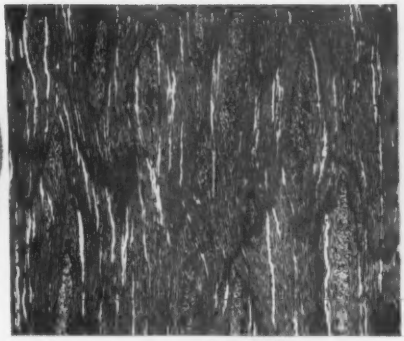

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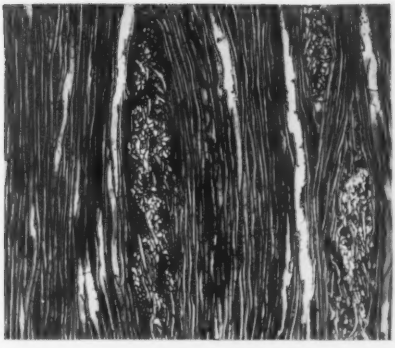

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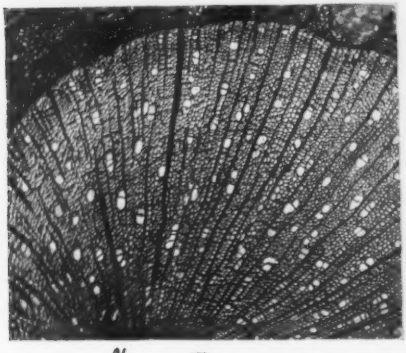

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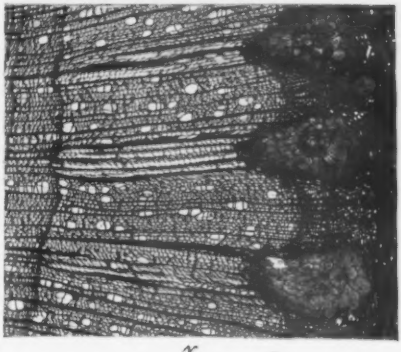

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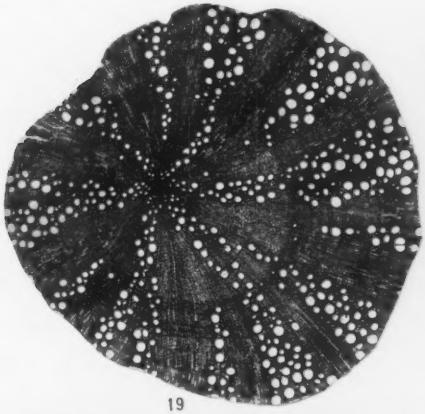
WHITAKER on BIRCH and OAK



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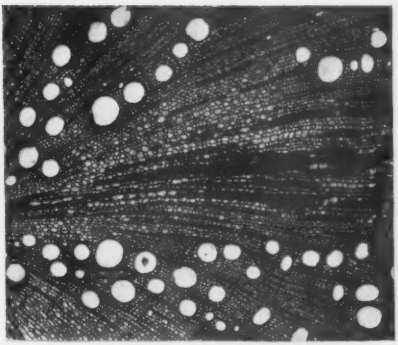

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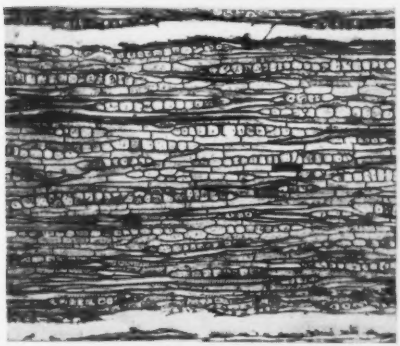

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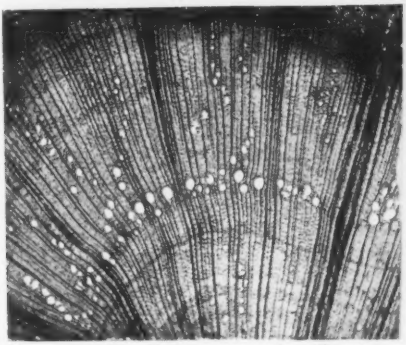

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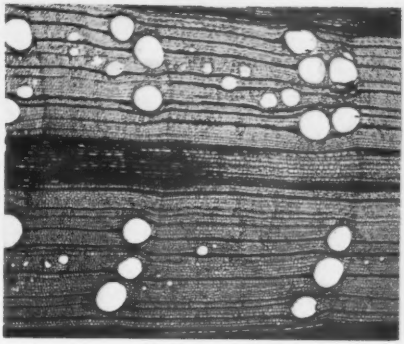

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WHITAKER on BIRCH and OAK

FIG. 16.—Transverse section of wounded seedling stem of *B. papyrifera.*

FIG. 17.—Part of same in wound cap, more highly magnified, showing diffuse type of ray structure.

FIG. 18.—Part of same opposite wound, showing aggregate character of rays.

PLATE XV

FIG. 19.—Transverse section of root of *Quercus rubra.*

FIG. 20.—Part of same more highly magnified, illustrating aggregate character of ray organization and showing transformation into parenchyma t aking place in central part of ray.

FIG. 21.—Tangential section through root of *Q. rubra,* showing aggregate ray structure.

FIG. 22.—Transverse section of wounded stem of *Q. velutina.*

FIG. 23.—Part of same through wound cap, more highly magnified to show aggregate rays.

FIG. 24.—Transverse section through wound cap of another specimen of same species, showing transformation from aggregate to compound type of ray organization.

BRIEFER ARTICLES

JOHN MACOUN

(WITH PORTRAIT)

Professor JOHN MACOUN, the well known Canadian naturalist, died July 18, 1920, at Sidney, British Columbia, after a long career in natural science, having given much to the world and brought great credit to the Dominion and to himself.

Being equally well versed in zoology and botany, his death is a severe loss to natural science. Even at the age of 89 years, Professor MACOUN was still active, and never lost his energy and interest for his science. He was born near Belfast, Ireland, in 1831, and came to Canada in 1850, when 20 years of age, with his mother and two brothers, and the family settled near Campbellford, Northumberland County. For a number of years Professor MACOUN taught school, and became professor of natural science at Albert College in Belleville. The greater part of his work was the exploration of the then unknown west; in 1872 he was invited by Sir SANFORD FLEMING, the supervising engineer, to accompany him as botanist in a tour across Canada, in connection with the surveys for the proposed Pacific railway. This tour forms the theme of Principal GEORGE M. GRANT'S well known *Ocean to ocean*, Dr. GRANT being one of the party. In 1875 Professor MACOUN accompanied Dr. SELWYN on the expedition to the Peace River District, where he made extensive collections of plants and animals for the Museum at Ottawa. Four years later, in 1879, he was sent by Sir CHARLES TUPPER to the north-

west to make some observations, and then began the collection of data upon which the *Catalogue of Canadian birds* is based, and which is the standard authority on that subject. The summers of 1879 and 1880 were spent on the prairies, ten parties having been sent to examine the country and ascertain its possibilities. Professor MACOUN was actively engaged in those two years, and in 1881 spent a considerable time in northern Manitoba. This long apprenticeship for the government service secured his appointment to the Geological and Natural History Survey in January, 1882, and the summers of 1882 and 1883 were spent around the lower St. Lawrence. In 1884 Professor MACOUN was located at Lake Nipigon, and in 1885 came back to British Columbia, operating in the Selkirks and Rockies. In 1887 he came to Vancouver Island again, and the next year moved to the Atlantic, working in Prince Edward Island in 1888. He was then promoted to assistant director and naturalist of the Survey, which position he continued to fill for many years. Since then Professor MACOUN made several long excursions to the East and West, and had the opportunity to even visit the little known Yukon Valley. In 1912 Professor MACOUN moved to Sidney, British Columbia, where he resided until his death.

The scientific work of Professor MACOUN covers a wide range in botany and zoology. He was remarkably gifted as an observer and collector. As an author botanists are familiar with his numerous publications on natural science, among which the *Catalogue of Canadian plants* is to his credit, representing an immense amount of work done by himself and his faithful assistant, his son, the late JAMES M. MACOUN. Both father and son devoted all their time to the development of natural science in Canada. The work they have left is an ample testimony of their united labors to promote science, and by their death the Canadian Dominion has lost two of its most brilliant and faithful servants.—THEO. HOLM, *Clinton, Md.*

CURRENT LITERATURE

BOOK REVIEWS

New text books of paleobotany

The first volume of SCOTT'S *Studies*[1] appeared in the third edition during the autumn of 1920. The present volume treats of the Pteridophytes, and includes a new chapter on the recently discovered early Devonian Psilophytales from the Rhymie chert bed in Scotland. Other additions are an account of the Lycopodineous fructification *Mazocarpon* and further information about the leaves of Calamites, the roots of *Sphenophyllum*, and the root zone in *Psaronius*. The chapter on the Botryopterideae is completely rewritten, in accordance with the recent discoveries by PAUL BERTRAND, KIDSTON, and GORDON. It is to be hoped that the next volume containing the Gymnosperms will soon appear. SCOTT'S *Studies* is unquestionably the most thorough treatment of fossil plants for the student of morphology, and the great value of the book is increased by the large number of excellent illustrations to which the author has devoted his careful attention in the successive editions.

No other text book of paleobotany has reached three editions, and only one was published a second time. This is POTONIÉ'S *Lehrbuch*,[2] which is now being re-edited by POTONIÉ'S successor, W. GOTHAN in Berlin. It has been carried as far as the Coniferales, and when completed will probably include the only modern treatment of Angiosperms in the literature of fossil botany. It is really an entirely new book, completely rewritten after POTONIÉ'S death (1917). The illustrations are well chosen and numerous, and, in accordance with POTONIÉ'S and GOTHAN'S training as state geologists of Prussia, attention is paid to the geologic history of plants, although stratigraphic observations are merely scattered through the text and not combined into independent chapters. A fairly complete treatment of the stratigraphic aspects of paleobotany would be highly desirable if offered in the yet unpublished portions of the book.

For the present we possess a short survey of stratigraphic paleobotany in up-to-date form only in BERRY'S last publication,[3] whose second part deals

[1] SCOTT, D. H., Studies in fossil botany. 3d ed. Vol. I. 8vo. pp. vi+434. *figs. 190.* London. 1920.

[2] POTONIÉ'S Lehrbuch der Paläobotanik. 2. Umgearbeitete Auflage von W. Gothan. Erste und zweite Lieferung. Berlin. 1919–1920.

[3] BERRY, E. W., Poleobotany: A sketch of the origin and evolution of floras. From the Smithsonian Report for 1918. pp. 289–407. *pls. 6.* Washington. 1920.

with this topic, while in the first part the status of biological paleobotany is outlined. How welcome a new presentation of the geologic history of plants must be to any paleontologist we can conclude from the fact that the only available books on the subject are W. P. SCHIMPER's *Traité de paleontologié végétale* (1869–1874) and Sir J. WILLIAM DAWSON's *Geological history of plants* (1888). Both books are out of date now. BERRY is probably the only living paleobotanist who could give us an exhaustive treatment of our present knowledge of fossil plants, including the Angiosperms, and of their geological distribution. It is to be hoped that his *Sketch* may soon be followed by a fuller treatment of the same subject.

No survey of the latest general treatises on paleobotany would be approximately complete without paying due respect to the concluding volumes of SEWARD's great reference book,[4] which represents the most exhaustive treatment of our present information on fossil Cryptogams and Gymnosperms. The last two volumes deal with the Pteridosperms, Cycadofilicales, Cordaitales, Cycadophyta, Ginkgoales, Coniferales, and Gnetales, to use SEWARD's own terminology. His book will remain for a long time the standard work on fossil botany and the main reference book for the students of this subject. The author promises in his preface to the fourth volume to publish in an independent volume a general review of the floras of the past, and the energy which allowed him to complete his monumental work after it had been started twenty-one years ago gives hope that he may fulfil his promise in the near future. The fact that neither SCOTT nor SEWARD dared to attack the intricate problems of the fossil Angiosperms shows clearly how much this great plant division is still in need of investigation. The morphological treatment of fossil Pteridophytes and Gymnosperms has lately absorbed the main attention of paleobotanists, to the great detriment of the higher orders. It is very much to be desired that this deficiency should soon be corrected.—A. C. NOÉ.

Botany of Iceland

The first part of the second volume of this publication, under the editorship of ROSENVINGE and WARMING, includes contributions by ØSTRUP[5], and GALLØE.[6] ØSTRUP has investigated the fresh-water diatom material of Copenhagen University, which had been assembled by 16 collectors. The list includes 468 species in 40 genera, 55 of the species being described as new. An instructive tabular survey of distribution is given under the two general heads of "universal distribution" and "distribution in the different parts of Iceland." The table shows that 95 per cent of the Icelandic forms occur in the rest of Europe, and about 50 per cent in Asia and America. In the arctic

[4] SEWARD, A. C., Fossil plants. Vols. III and IV. Cambridge. 1917 and 1919.

[5] ØSTRUP, ERNST, Fresh-water diatoms from Iceland. pp. 1–98. *pls.* 5. 1920.

[6] GALLØE, OLAF, The lichen flora and lichen vegetation of Iceland. pp. 101–247. 1920.

regions, Greenland "stands highest," with 41 per cent of the Icelandic forms, but the total number of species in Iceland exceeds that of any other arctic region.

GALLØE presents the lichen flora under six aspects: (1) a list of species (284 species in 55 genera); (2) the means of propagation and dispersal; (3) the "biology" under four categories, bark lichens, epiphyllous lichens, earth lichens, and rock lichens; (4) the classification of the lichens into associations; (5) the vertical distribution of the lichens; and (6) the abundance of lichens in Iceland. The classification into associations is based upon the character of the substratum and of the vascular plants. Iceland is shown to have a lichen vegetation poor in species in proportion to its area. Epiphyllous lichens are entirely lacking in such a climate, and bark lichens are scanty in their occurrence. On the contrary, the conditions for the development of earth and rock lichens are better than in the temperate or tropical regions. It follows that, in spite of the rigorous climate, the soil and rocks show a large number of specimens. The lack of data regarding moss development is regretted, and an effort is made to remedy it by presenting the frequency of occurrence according to the RAUNKIAER method.—J. M. C.

MINOR NOTICES

North American flora.—The fourth part of Volume 7 continues the Aecidiaceae by J. C. ARTHUR, who in collaboration with F. D. FROMME presents *Dicaeoma* on Poaceae, 88 of the 269 species listed in the analytical key being included in the present part, 43 of the names being new combinations. The tangle of synonymy involved in such a group is very impressive.—J. M. C.

NOTES FOR STUDENTS

Taxonomic notes.—BRITTON,[7] in collaboration with several botanists, has published descriptions of 170 new species of Cuban plants, distributed among many families, and including 10 new genera as follows: *Bembicidium* and *Cãnizatesia* in Leguminosae; *Ramsdenia*, *Roigia*, and *Dimorphocladium* in Euphorbiaceae; *Cheilophyllum*, *Silvinula*, *Naiadothrix*, and *Anisantherina* in Scrophulariaceae; and *Cotema* in Bignoniaceae.

WILLIAMS,[8] in anticipation of publication in the *North American flora*, has presented the results of his study of the Calymperaceae, "partly to allow the illustration of cross-sections of the leaves to be issued with the descriptions." This family of mosses includes only the genera *Syrrhopodon* and *Calymperes*, the former containing 18 species (1 new) and the latter 12 species (3 new).

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[7] BRITTON, N. L., Descriptions of Cuban plants new to science. Mem. Torr. Bot. Club **16**:57–118. 1920.

[8] WILLIAMS, R. S., Calymperaceae of North America. Bull. Torr. Bot. Club **47**:367–396. *pls. 15–17*. 1920.

ARTHUR,[9] in his twelfth paper describing new species of Uredineae, has published 19 new species, 12 of which are under *Aecidium*. In addition, there are several new combinations and new names.

HITCHCOCK[10] has published revisions of the four genera of Paniceae: *Isachne* (8 spp.), *Oplismenus* (4 spp.), *Echinochloa* (7 spp.), and *Chaetochloa* (26 spp.). Full synonymy, often very extensive, and distribution are given in addition to the detailed descriptions. Although no new species are described, there are many transfers.

STANDLEY[11] has begun the publication of an account of the trees and shrubs of Mexico, the first paper extending from Gleicheniaceae to Betulaceae, certain families being contributed by specialists. In addition to a general explanatory introduction, there is an interesting history of botanical exploration in Mexico. The Pteridophytes are represented by 28 species, and the Gymnosperms by 56, *Pinus* being credited with 26. The largest genus included is *Agave*, presented by TRELEASE. It is credited with 170 species, 31 of which are described as new. Since 46 other species are credited to TRELEASE, his relationship to the genus is obvious. The next largest genus is *Piper*, with 59 species, the majority of which are credited to the late CASIMIR DE CANDOLLE.

FITZPATRICK[12] has published a detailed monograph of the Coryneliaceae (Perisporiales), the majority of whose species occur only in tropical or subtropical regions. The family includes 14 species, representing 4 genera. The largest genus is *Corynelia*, with 9 species, 5 of which are described as new.

PENNELL[13] has begun the publication of his studies of the Scrophulariaceae of Colombia, based on an exploration of the region for a period of eight months during 1917 and 1918. The first paper includes the Antirrhinoideae, in which 23 genera are recognized, 2 of them being described as new (*Monocardia* and *Unanuea*). Much the largest genus is *Fagelia*, with 18 species (10 new), all the other 22 genera including 31 species (12 new).

BURT,[14] in his twelfth paper on the Thelephoraceae of North America, presents the genus *Stereum*, recognizing 77 species, 12 of which are new.

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[9] ARTHUR, J. C., New species of Uredineae. XII. Bull. Torr. Bot. Club **47**: 465–480. 1920.

[10] HITCHCOCK, A. S., Revisions of North American grasses: *Isachne*, *Oplismenus*, *Echinochloa*, and *Chaetochloa*. Contrib. U.S. Nat. Herb. **22**:115–208. *pls. 25–32. figs. 21–62.* 1920.

[11] STANDLEY, P. C., Trees and shrubs of Mexico (Gleicheniaceae-Betulaceae). Contrib. U.S. Nat. Herb. **23**:1–169. 1920.

[12] FITZPATRICK, H. M., Monograph of the Coryneliaceae. Mycol. **12**:206–267. *pls. 12–18.* 1920.

[13] PENNELL, F. W., Scrophulariaceae of Colombia. I. Proc. Acad. Nat. Sci. Philadelphia **72**:136–188. 1920.

[14] BURT, E. A., The Thelephoraceae of North America. XII. Ann. Mo. Bot Gard. **7**:81–240. *pls. 9.* 1920.

The full descriptions, detailed lists of stations, and numerous text cuts leave nothing to be desired in the way of information.

MAXON[15] has described 6 new species of *Selaginella* from southern California, New Mexico, Arizona, and Glacier National Park.

WILDEMAN[16] has published another fascicle of additions to the flora of the Congo, illustrating the abundance of material that continues to be discovered in that interesting territory. A full list of collectors and stations is given, and frequently also full descriptions based upon fresh material. There is also included an account of *Meliola* as represented in the Congo country, with descriptions of new species and varieties, and *Meliolinopsis* is established as a new genus.

ROBINSON,[17] in connection with his study of the Bolivian representatives of *Eupatorium*, has described certain novelties of the tribe. New species are described in *Micania* (19), *Eupatorium* (6), *Ageratum*, and *Alomia*, while *Sphaereupatorium* is established as a new genus and credited to KUNTZE. In the Eupatoriums of Bolivia, 68 species are recognized, 29 of which are endemic. In this connection the following statement is made: "The endemism of Bolivia as illustrated by this group is thus about 43 per cent as against about 55 per cent in Peru and 59 per cent in Colombia. After deducting the 29 endemic species, there remain 39 Bolivian Eupatoriums which extend to other countries. Of these only 18 are known in Peru, while nearly all the others are species common to south-central Brazil and northern Argentina. Beyond a very few species of wide distribution there is a surprisingly slight common element between the Bolivian and Paraguayan members of the genus, although *Eupatorium* is pretty well represented in both of these contiguous countries." —J. M. C.

Reproduction of Douglas fir forests.—The great importance of the Douglas fir forest region may be appreciated from the estimate by MUNGER[18] that the stand within Washington and Oregon amounts to 560 billion feet of merchantable timber, while the amount in the adjacent forests of British Columbia according to WHITFORD[19] is not less than 350 billion feet. It seems certain that the amount destroyed by comparatively recent fires is almost if not quite

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[15] MAXON, W. R., New Selaginellas from the western United States. Smithson. Miscell. Coll. **72**: no. 5. pp. 10. *pls. 6*. 1920.

[16] WILDEMAN, E. DE, Additions à la flore du Congo. Bull. Jard. Bot. Bruxelles **7**:1–160. 1920.

[17] ROBINSON, B. L., I. Further diagnoses and notes on tropical American Eupatorieae. II. The Eupatoriums of Bolivia. Contrib. Gray Herb. New Series. no. 61. pp. 80. 1920.

[18] MUNGER, T. T., Forestry in the Douglas fir region. Amer. Forestry **26**:199–205. *figs. 7*. 1920.

[19] WHITFORD, H. N., and CRAIG, R. D., Forests of British Columbia. pp. 409. *pls. 28. maps 21*. Commission of Conservation, Canada. Ottawa. 1918.

equal to that now standing. The character and extent of the destruction are indicated by MUNGER, and have been given in more detail by HOFMANN[20] in a most interesting article. A great burn occurring in 1902 in south-central Washington, and devastating more than half a million acres, was made the site of an important investigation of some of the problems of natural reforestation. The resulting report[21] shows the importance of a careful ecological study of all the factors concerned. In spite of the complete and apparently hopeless desolation succeeding this fire, typical of hundreds of similar conflagrations in the Douglas fir region, HOFMANN found that a good even-aged stand of reproduction immediately followed. This extended over the greater portion of the devastated area, regardless of the presence or absence of surviving seed trees, and was shown to be due to an abundance of seed stored in the duff of the forest floor and retaining its viability through the fire. The efficiency of seed trees in restocking the ground was found to be limited to a radius not exceeding 300 feet from the parent tree, hence they were not important in the reforestation of so large an area. Local failure in reforestation within this area was found to be due either to the complete destruction of all the duff, with its contained seed, over certain portions of the area and more particularly upon the drier southern slopes, or to the occurrence of a second fire after all the viable stored seed had germinated. This resulted in the destruction of all the seedlings before they were old enough to bear seed to restock the forest floor. The burial of seeds and cones by rodents was found to be an important factor in stocking the duff.

More recent investigations by HOFMANN[22] of the ecology of these forests show the *Pseudotsuga* to be unable to withstand shade, and hence to constitute the principal member of a pioneer forest of which *Thuja* and *Tsuga* form the climax. The characteristics of the Douglas fir which give it such a prominent place in the Washington and British Columbia region are given as follows: "The production of heavy crops of seed which is the favorite food of the indigenous rodents; caching of seed by rodents in the forest floor; ability of the seed to retain its viability while stored in the forest floor and to live through forest fires; early and quick germination of the seed under favorable conditions; and a rapid development of a long radicle."

Many of these factors are somewhat within the control of man, and upon them the scientific management of Douglas fir forests must be based. Such a system has been described by MUNGER (*loc. cit.*) and in its bare outline consists in: (1) logging clean, (2) falling dead trees or "snags," which

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[20] HOFMANN, J. V., How fires destroy our forests. Amer. Forestry **26**:329–336. *figs.* 7. 1920.

[21] ———, Natural reproduction from seed stored in the forest floor. Jour. Agric. Res. **11**:1–26. *pls.* 7. 1917.

[22] ———, The establishment of a Douglas fir forest. Ecology **1**:49–53. *fig.* 1. 1920.

are a fire menace, (3) burning the slash broadcast the first spring or fall after logging, and (4) keeping subsequent fires out of all areas once burned. These constitute the methods now followed within the national forests of Washington and Oregon to secure the reforestation of lumbered areas.—GEO. D. FULLER.

Plants of acid soils.—A method of determining the acidity or alkalinity of soils according to the hydrogen-ion concentration, and adapted to use in the field, has been developed by WHERRY.[23] He has also used the method in determining the character of the soil in which certain "oxylophytes" are usually found growing.[24] Based upon the reaction of the soil solution, the soils were classified for the purpose of this study as "superacid," "mediacid," "subacid," and "minimacid," containing respectively more than 1000 times the acid of pure water, 100 to 1000 times, 10 to 100 times, and up to 10 times, with a similar evaluation of the alkaline soils. It is then pointed out that oxylophytes may be regarded as plants of mediacid soils and calcicoles of neutral or minimalkaline soils. Tables based upon soil tests show that among the heath plants of New England, those of the Pyroloideae are most characteristic of subacid soils, while the Ericoideae and Vaccinoideae most usually reach best development upon mediacid soils, many upon subacid and minimacid soils, and a few upon neutral soils. A further list of plants upon mediacid soils includes such species as *Aspidium spinulosum*, *Lycopodium Selago*, *Clintonia borealis*, *Coptis trifolia*, *Cornus canadensis*, and *Linnaea borealis*. Another list is compiled of plants upon circumneutral soils.

Similar methods applied to the study of certain coastal areas also give most interesting results.[25] A strip of land between the pine barrens and the salt marshes of New Jersey and populated by plants characteristic of the upland woods of the northern part of the state showed a specific acidity of 10 or less, so that the soil may be classified as circumneutral. On closely associated areas are found plants which grow elsewhere in southern New Jersey only in the sand barrens. These soils, in spite of their proximity to the salt marsh, showed a specific acidity of 300, or practically the same as that of the pine barren sands themselves. The border of some salt marshes on the Massachusetts coast showed plant associations usually found inland on peat or wet sand, and again tests proved the soil to be strongly acid. The explanation of these strongly acid soils bordering the alkaline salt marsh areas is that from the sea water drawn by capillarity into the soil the bases

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[23] WHERRY, EDGAR T., Determining soil acidity and alkalinity by indicators in the field. Jour. Wash. Acad. Sci. **10**:217–223. 1920.

———, Soil acidity and a field method of its measurement. Ecology **1**:160–173. *pl. 1.* 1920.

[24] ———, Soil tests of Ericaceae and other reaction-sensitive families in northern Vermont and New Hampshire. Rhodora **22**:33–49. 1920.

[25] ———, Plant distribution around salt marshes in relation to soil acidity. Ecology **1**:42–48. 1920.

are adsorbed by the clay and humus, and the acids set free. In such areas the reaction is often found to change sharply within a few centimeters from a specific alkalinity of 30 to a specific acidity of 300. These methods and results seem likely to place the old contention of the relative importance of the physical and chemical properties of soil upon a new experimental basis, and to result in a much clearer conception of the meaning and application of the terms "oxylophytes" and "calcicoles."—GEO. D. FULLER.

Seacoast vegetation.—A description of the vegetation of the eroding seashores of Connecticut has been added by NICHOLS[26] to his other studies of the vegetation of the state previously noted in this journal.[27] He groups the important factors as those relating to submergence, such as salinity, tides, illumination, and temperature of the water, those relating to physiography, and those to atmospheric influences. The eroding seashores of the state are developed either in rock or glacial drift, and from each of these situations distinctive associations are described. The range of the studies is from the sublittoral algal associations to the forests which fringe the shores.

The depositing shores present even more diverse conditions,[28] depending principally upon the character of the soil, stony, sandy, and muddy areas, each having characteristic series of associations. The various associations are carefully described, and in the actual succession along muddy shores there is found evidence of coastal subsidence similar to that presented by GANONG, PENHALLOW, BARTLETT, and others.

Some attention is devoted to the salt marsh depressions or "pans" which appear to have various origins. Some are due to the destruction of the ordinary salt marsh vegetation by the decay of masses of plant remains swept over the surface during times of unusually high water, but others result from the partial filling and obstructing of tidal creeks and lagoons or by the building of tidal levees and the consequent ponding of water, between tides, in the lower parts of the marsh.—GEO. D. FULLER.

Crown gall of alfalfa.—WILSON[29] has described and figured in some detail the fungus causing crown gall of alfalfa. He concludes that the parasite is present in the gall in the form of a plasmodium, formed by the fusion of amoeboid cells in the host cells. He thinks that it spreads through the host tissues as a streaming mass or network of naked protoplasm, and that any mycelium observed has no connection with the gall forming organism. This plasmodial

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[26] NICHOLS, GEO. E., The vegetation of Connecticut. VI. The plant associations of eroding areas along the seacoast. Bull. Torr. Bot. Club **47**:89–117. *fig. 6.* 1920.

[27] ———, BOT. GAZ. **59**:159–160. 1915; **65**:572. 1918.

[28] ———, The vegetation of Connecticut. VII. The associations of depositing areas along the seacoast. Bull. Torr. Bot. Club **47**:511–548. *fig. 10.* 1920.

[29] BOT. GAZ. **70**:51. 1920.

state of the fungus was not observed by VON LAGERHEIM,[30] or by MAGNUS,[31] and has never been found by the reviewer. Even at a very early stage a definite mycelium appears to be present in the host plant, the hyphae of which are bounded by a thin wall. The ends of these hyphae form small swellings or vesicles which are active in dissolving the walls of the host cells. The method of branching of the hyphae and the development of the resting spore have been studied, and they seem to agree very closely with the descriptions given by SCHROETER,[32] MAGNUS, and VON LAGERHEIM for this fungus and for others which they consider closely allied to it. It is hoped to publish shortly a full account of this investigation and of a number of infection experiments undertaken in connection with several outbreaks of the disease in this country.—JAMES LINE, *Botany School, Cambridge, England.*

Radio-active material.—BLACKMAN[33] gives an extremely clear statement of the possible significance of radio-activity in normal physiological processes. He discusses mainly the work of the Dutch investigator H. ZWAARDEMAKER (Jour. Physiol. **53**: 273–289. 1920), in which he found that various radio-active materials would maintain or induce heartbeat in a potassium-free Ringer solution. This is taken as evidence that the effectiveness of potassium salts on heartbeat is due to the radio-activity of potassium, for in equal radio-active concentration uranium and radium were equally effective with potassium. Potassium gives only β-radiations. Elements that emit only α-radiations were also effective in inducing and effecting heartbeat.

"The mode of action of these corpuscular radiations is not clear. The charged particles as they shoot along will act by induction, detaching everywhere electrons from these atoms; they also transfer kinetic energy, and when they come to rest on, say, some colloidal complex of the cell, they will transfer their electric charge and so may set free some ion absorbed on the surface. Whatever the nature of the action, ZWAARDEMAKER concludes that radio-activity is a mighty biological factor capable of restoring a lost function." BLACKMAN believes that this may explain, in part, the function of potassium in the plant.—WM. CROCKER.

Subalpine lake shore vegetation.—To his already extensive studies of Colorado mountain vegetation, RAMALEY[34] has recently added a report based upon a ten years' study of numerous subalpine lakes located at altitudes of 10,000–11,300 ft. in the Rocky Mountains of Colorado. Data are presented

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[30] VON LAGERHEIM, G., Bihang K. Svenska Vet. Akad. Hand. **24**: no. 4. 1898.

[31] MAGNUS, P., Ann. Botany **11**: 87. 1897; Ber. Deutsch. Bot. Gesells. **20**: 291–296.

[32] SCHROETER, J., Bot. Centralbl. **11**: 219–221. 1882.

[33] BLACKMAN, V. H., Radio-activity and normal physiological function. Ann. Botany **34**: 299–302. 1920.

[34] RAMALEY, F., Subalpine lake shore vegetation in north central Colorado. Amer. Jour. Bot. **7**: 57–74. *figs. 6.* 1920.

regarding topography, climate, and soil, and the typical zonation of the vegetation is outlined. These lakes are within the limits of the *Picea Engelmanni* forest, and the succession from the water's edge includes moor, heath, and meadow associations. Different expressions of these types are to be seen about the various lakes, the moor, with its variations of moss moor, sedge moor, rush moor, willow moor, and meadow moor, usually occupying a large proportion of the area. Perhaps the most interesting of the communities is the heath, in which *Gaultheria humifusa*, *Vaccinium caespitosum*, and *Kalmia microphylla* are conspicuous. Any one of these small undershrubs or a combination of all three may dominate a comparatively narrow belt of vegetation midway between the lake and the forest. The several aspects of the associations are noted, the meadows affording the most brilliant and varied display. Maps, diagrams, quadrats, and lists of species make the report graphic and exact.—GEO. D. FULLER.

Accessory foods for plants.—BOTTOMLEY[35] has found several chlorophyll bearing water plants unable to develop normally in nutrient salt solutions not bearing accessory organic foods. The plants worked on were as follows, naming them in descending order of their dependence upon the organic material: *Lemna major* and *L. minor*, *Salvinia natans*, *Azolla filiculoides*, and *Limnobium stoloniferum*.

"The effective organic substances were found to be present in an autoclaved growth of *Azotobacter chroococcum*, crude nucleic acid derivatives from raw peat, and a water extract of bacterized peat. . . . . In no case did the organic substance supplied exceed 184 parts per million, while the concentration of inorganic salts in the culture solution totaled 5500 parts per million."

The author thinks that these plants in nature secure their necessary organic materials from the waters in which they grow. From the work of BOTTOMLEY and of several other investigators who have recently published their results, it appears that accessory foods may have considerable significance in plant development, as they have very great significance in animal nutrition and growth.—WM. CROCKER.

Rate of photosynthesis in the field—MCLEAN[36] of the Philippines has worked up a simple method of measuring the amount of carbon dioxide absorbed by leaves in the open. There is certainly great need of such methods for determining photosynthetic rates as well as the rates of other plant processes occurring in the field. Recently a farmer who had fertilized heavily with rock phosphate and limestone asked why his corn with about the same foliage stores more than twice as much starch in the ears as his neighbor's corn for

[35] BOTTOMLEY, W. B., The effect of organic matter on the growth of various water plants in culture solutions. Ann. Botany **34**:353–365. 1920.

[36] MCLEAN, F. T., Field studies of the carbon dioxide absorption of coconut leaves. Ann. Botany **34**:367–389. 1920.

which no phosphate or lime was used. Good field methods along with laboratory methods are necessary for answering such questions.

McLEAN finds that middle aged leaves of the coconut absorb carbon dioxide faster than either immature or old leaves. These leaves also show a maximum in the morning, a depression at midday, a second rise in the afternoon, followed by the final decline at sunset. Detached coconut leaves showed about the same rate of absorption as attached ones, but the maxima occurred at different times of day. Sugar-cane leaves absorb much more rapidly than coconut.—WM. CROCKER.

Nitrites and nitrates in plants.—STROWD[37] has worked on the relative accuracy of various methods for determining nitrites and nitrates in plant tissues. He finds that both the Devarda and Schloesing methods with proper modifications give fair accuracy. Various other methods tried proved unsatisfactory. STROWD[38] also finds strong evidence that the reason for failure of nodule production (in soy bean) in the presence of nitrates is due at least in part to the effect of the high concentration of nitrate in the sap upon the growth and reproduction of *Rhizobium leguminosarum*. He finds that the amount of sugar present decreased with an increase in nitrates, but that some sugar was always present. It is unknown to what extent shortage of sugar is significant. The concentration of nitrates in the roots is far in excess of the concentration in the soil bathing the roots.—WM. CROCKER.

Humidity and irrigation.—In the Imperial Valley, California, the irrigation of 400,000 acres of arid lands is commonly supposed to have been accompanied by a decided increase in atmospheric humidity. That this is not the case is shown by data collected by McGREGOR,[39] who concludes that no appreciable influence is exerted upon atmospheric humidity by the amount of irrigation water used, seasonal fluctuations in humidity being accounted for through factors of much greater geographical extent.—GEO. D. FULLER.

Conifer grafting.—The case of a natural grafting of spruce upon pine is reported by ROMELL,[40] who has also investigated the nature of the union as seen in the structure of the wood cells. Along the line of contact there was found evidence of the character of the pits of each being influenced by the proximity of the tissues of the other.—GEO. D. FULLER.

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[37] STROWD, W. H., The determination of nitrites and nitrates in plant tissue. Soil Science **10**:333–342. 1920.

[38] ———, The relation of nitrates to nodule production. Soil Science **10**:343–356. 1920.

[39] McGREGOR, E. A., The relation of irrigation to humidity in a recently reclaimed desert. Plant World **22**:45–52. *figs. 3*. 1919.

[40] ROMELL, LARS-GUNNAR, Anatomy of a grafting of spruce on pine. Meddel. Från Statens Skogsförs. **16**:61–66. *figs. 2*. 1919.

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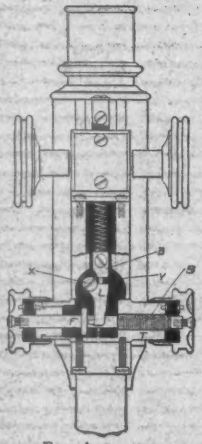

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